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UNIVERSITY OF NORTHERN COLORADO

Greeley, Colorado

The Graduate School

CLONAL GROWTH AND TRAIT VARIATION IN THE
COLORADO FRONT RANGE: THE INFLUENCE
OF ELEVATION AND ECOSYSTEM

A Thesis Submitted in Partial Fulfillment
of the Requirements for the Degree of
Master of Science

Jordan Nicole Conley

College of Natural and Health Sciences
Biological Sciences
MS-Thesis in Biological Sciences

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This Thesis by: Jordan Conley

Entitled: *Clonal Growth and Trait Variation in the Colorado Front Range: The Influence of Elevation and Ecosystem*

has been approved at meeting the requirement for the Degree Master of Science in the College of Natural and Health Sciences in the Department of Biological Sciences.

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ABSTRACT

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Amid global climate change, exploring adaptive strategies among alpine flora, particularly through clonal growth, becomes critical for biodiversity conservation. This study aims to explore the patterns of dominance and distributions among clonal species across environmental gradients in the Colorado Front Range, employing a trait-based comparative analysis to understand the adaptive strategies of alpine flora and their implications for conservation amid rapid climate change. We focused on two species, studying traits like lateral spread, bud count, and bulbil numbers. Advanced statistical methods such as Permutational Multivariate Analysis of Variance (PerMANOVA) and Multi-Response Permutation Procedures (MRPP) were used to evaluate community compositions and biodiversity variations across the gradient. Results confirmed significant variations in community composition, influenced by ecosystem type and elevation, highlighting the importance of these factors in defining plant communities. The research revealed a pronounced dominance of clonal growth in alpine and forest ecosystems, underscoring the complexity of clonal adaptation and survival strategies in response to environmental stresses. Unexpected patterns, such as the lateral spread in *Carex nardina*, demonstrate the intricate relationship between clonal growth patterns and environmental gradients. Acknowledging limitations such as the focus on broad environmental gradients and single-season data collection, future directions include collecting fine-scale environmental data and integrating genetic analyses to deepen understanding of clonal populations' genetic structure.

This thesis advances our understanding of adaptive strategies of alpine plants and emphasizes the need for a multidimensional approach in ecological research to effectively conserve biodiversity and develop predictive models in response to climate change.

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CHAPTER I

INTRODUCTION TO CLONAL GROWTH MECHANISMS, ENVIRONMENTAL GRADIENTS, AND ALPINE PLANT RESILIENCE IN A CHANGING CLIMATE

Clonal growth, a widespread, but often overlooked strategy of plant ecology, is a mechanism that allows plants to reproduce vegetatively, producing genetically identical daughter ramets (i.e. clones). The significance of studying clonal plants, particularly in the context of plant traits and their adaptive strategies, becomes evident when considering the work of Herben et al. (2015) and Chelli et al. (2019), which explore the trade-offs and environmental constraints of clonal growth. These studies highlight how clonal plants often exhibit lower reproductive rates but may capitalize on their abilities in lower-quality ecosystems, with climate being a major driver of clonal and bud bank traits. Clonal reproductive strategies are particularly significant for plant species inhabiting harsh or rapidly changing environments, such as high-elevation alpine ecosystems, where it may provide plants with a collection of adaptive advantages. Clonal plants, characterized by their diverse clonal growth organs (CGOs), can exploit their habitats efficiently, enabling persistence and spread even in competitive and resource-limited conditions. The ability to utilize vegetative growth to forage for resources, occupy space, or share resources between connected ramets, enhance survival and competitiveness of clonal plants. The integration of clonal traits within the community structure is a critical aspect of ecosystem dynamics, potentially enhancing the resilience of plant communities against environmental fluctuations. Examining clonal traits across various environmental gradients is crucial. This study utilizes the

elevation gradient, where changes in distinct climatic conditions affect plant community composition and function. Given the importance of clonal traits, it is essential to understand how their role in the community and within a species, changes across various environmental gradients, especially in light of ongoing climatic changes.

Plant traits, in general, offer insights into the strategies species employ to survive, grow, and reproduce under diverse environmental conditions. Focusing on clonal traits sheds light on under what circumstances these are advantages or disadvantages. Alpine ecosystems, characterized by cold temperatures and short growing seasons, support specialized and often endemic plant species whose primary production is inherently limited (Munson & Sher, 2015). The traits associated with clonal growth—such as lateral spread and bud bank size—are vital for these plants' adaptive capacity. These traits enable them to respond to environmental fluctuations, contributing to their performance and dominance within their respective communities (Klimeš, 2008). However, the benefits of clonal traits may come with trade-offs, particularly in energy allocation, affecting growth and reproductive strategies (Herben et al., 2015), emphasizing the complexity of clonal growth in plant adaptation and survival strategies.

As the Earth's climate continues to undergo significant and rapid changes – including shifts in temperature, precipitation patterns, and extreme weather events, alpine ecosystems are particularly vulnerable. The Colorado Front Range, a region within the Rocky Mountains, has already exhibited signs of such climate-driven transformations (Bueno de Mesquita et al., 2020; Kittel et al., 2015; Pepin & Losleben, 2002). Mountains serve as ideal models for studying climate change impacts, offering gradients that mirror the anticipated effects of global warming. Predicted warming trends at higher elevations and alterations in precipitation are expected to affect not only the phenology and geographic ranges of alpine vegetation but also the nature of

the ecosystems themselves. The rapid pace of these changes allows for little time for evolution to occur, highlighting the importance of plasticity and existing trait variability in species survival and resilience.

This literature review aims to synthesize current knowledge on how clonal growth traits interact with environmental gradients and their impact on plant performance and dominance, while also identifying gaps for future research. The questions guiding this review speak to the broader goal of understanding clonal plant strategies along an elevation gradient. Studying clonal traits provides a window into the adaptive strategies of plants facing the dual pressures of environmental variability and climate change, making it a pivotal area of ecological research. Understanding trait responses is crucial for informing conservation efforts and developing predictive vegetation models.

To explore the dynamics related to clonal strategies, this study aims to explore the patterns of dominance and distribution among clonal species across environmental gradients in the Colorado Front Range, employing a trait-based comparative analysis to understand the adaptive strategies of alpine flora and their implications for conservation amid rapid climate change. In doing so, the research aims to understand how variations in environmental conditions across this gradient influence both plant and clonal species' ability to dominate their ecosystems. As elevation increases, the environmental conditions shift dramatically, affecting the survival and reproductive strategies of plant species. We hypothesize that in the lower elevation forest ecosystems, where conditions are relatively mild and resources are plentiful, clonal plants may utilize their foraging abilities to dominate. Similarly, in alpine ecosystems clonal strategies may be more dominant due to the benefits of physiological integration between ramets and longevity. As climate change continues to alter temperature patterns, precipitation, and the frequency of

extreme weather events, the adaptive capacity of plant species, shaped significantly by their inherited and plastic traits, becomes a focal point of ecological research. This approach to understanding how plant traits respond under different environmental conditions is essential for predicting ecosystem responses to climate change, offering insights critical to the development of conservation and management strategies.

Research Questions

- Q1 How does plant dominance change across the environmental gradient?
- Q2 How does clonal dominance change across the environmental gradient?
- Q3 How does intraspecific clonal trait variation change across the environmental gradient?

Hypotheses

- H1 There will be a change in community composition across the gradient.
- H2 In alpine and forest ecosystems, clonal plants will be dominant in cover.
- H3 Clonal plants exhibit significant intraspecific trait variation across environmental gradients.

The findings of this literature review aim to contribute to the understanding of clonal plant strategies in high-elevation ecosystems, potentially informing conservation efforts and predictive models in the context of climate change.

Colorado Front Range

The Colorado Front Range serves as a natural laboratory for studying the impacts of climate change on alpine ecosystems. This region, characterized by its gradual elevation increase from the eastern lowlands towards the high peaks of the Rocky Mountains, exhibits a semi-arid climate marked by warm, dry summers and cold winters (Decker et al., 2020). This region's distinctive diurnal and seasonal temperature variations become more pronounced with elevation

gain, while precipitation patterns also increase, presenting a complex gradient of environmental conditions (Doesken et al., 2003; Kittel et al., 2015).

Colorado's mountains experience seasonal and diurnal temperature changes, with temperatures decreasing with elevation gain. In July, lower valleys may experience temperatures of around 70 to 80°F, while higher elevations are around 50 to 60°F (Doesken et al., 2003). At night, these areas may experience freezing temperatures, even during summer. During winter, it is anticipated that below-freezing temperatures will occur each year.

Precipitation generally increases with elevation gain. However, we can expect a changing climate to affect the amount of precipitation in the region. A study at the alpine station of Niwot Ridge found a 60 mm per decade increase in annual total precipitation, with an overall increase of 230 mm across the 1952 to 2010 record (Kittel et al., 2015). In contrast, Mote et al. (2005) identified a broader, regional decline in Snow Water Equivalent (SWE) across the western United States due to warming temperatures. Clow (2010) adds to this complexity by detailing how locations across Colorado have experienced earlier snowmelt, which could have significant implications for water availability throughout the year. These studies illustrate a nuanced picture: while specific high-elevation areas like Niwot Ridge may experience increased precipitation, broader regional climate change impacts, especially warming, are contributing to declining snowpacks and altered water availability.

Studies modeling future climate change effects in the Rocky Mountains generally predict that alpine ecosystems will experience more significant warming than those of lower elevations (Diaz & Eischeid, 2007; Fyfe & Flato, 1999; Snyder et al., 2002). However, when land-use practices were included, one model predicted high-elevation cooling rather than warming

(Stohlgren et al., 1998). Studies at Niwot Ridge support this prediction, showing absolute cooling above the treeline from 1952-1997 (Pepin, 2000; Pepin & Losleben, 2002).

More recently, another study performed at Niwot Ridge Long Term Ecological Research (LTER) site in the Front Range found that the 56-year record showed no significant cooling trends at the alpine site (McGuire et al., 2012). However, further analysis found that when only the 20-year record was considered, a uniform 0.4°C increase in mean temperature per decade was seen across the transect. From 1952 through the mid-1970s, there appeared to be a decrease in temperature (Pepin & Losleben, 2002; Williams et al., 1996). However, temperatures have increased since (Clow, 2010).

With a changing climate, high-elevation ecosystems are experiencing earlier snow melt and glacial retreat (Bueno de Mesquita et al., 2020). This change may allow plants to move into areas that were previously unvegetated, including those that were traditionally covered in snow. Additionally, this could result in a longer growing season.

However, the longer growing season is not the only factor to consider. Snowpack is essential for plant survival through the cold season. Earlier snowmelt correlates with colder spring temperatures and more frost events experienced by vegetation (Wipf et al., 2006). The loss of deep snowpack results in less insulation, causing soil temperatures to drop and plant tissues to be injured. The melting of snowpack may also serve as a phenological trigger, allowing for fresh growth to occur. Inouye (2008) found that more significant snowpack and later snowmelt results in a later start for plant growth and, therefore, less frost mortality of buds in subalpine wildflowers. Exposed plant tissues are left vulnerable to early-season frosts. However, clonal plants may have extensive bud banks belowground that enable them to regenerate more effectively after damage, taking advantage of an already established root system.

Additionally, phenological mismatches induced by altered snowmelt timing can disrupt plant-pollinator interactions, potentially leading to reproductive failures in plants that rely on animal pollination (Miller-Rushing et al., 2010). These mismatches are particularly concerning for alpine specialists that have co-evolved with specific pollinator species (CaraDonna et al., 2014). The observed phenological mismatches induced by altered snowmelt timing illustrate the importance of measuring asexual reproduction in alpine species. Clonal propagation could provide reproductive assurance under changing climate conditions.

The Alpine-Treeline Ecotone

The term ecotone refers to the area where bordering ecosystems overlap. This overlap forms a region that shares the characteristics of each ecosystem, though it may also have emergent properties and provide an opportunity for unique species occurrences. Thus, species found in an ecotone may be found in either ecosystem. Plants within the ecotone are likely tolerant to conditions of both ecosystems until their environmental limit is met (Humphries et al., 2007; Malanson et al., 2017). This location is where we may see a boundary, though there are typically several intermediate vegetation zones rather than an abrupt change due to species-specific environmental tolerances (Bourgeron et al., 2015). Since ecotones are the borders of ecosystems, they are vulnerable to shifting climatic conditions, eventually shifting the location of the ecotone as well.

The alpine-treeline ecotone is the transition zone between the forest and alpine vegetation. Somewhere within this zone is the treeline, the highest elevation at which trees can grow before conditions are too harsh and the abiotic threshold is reached. Additionally, there may be environmentally stunted or deformed trees present, commonly referred to as krummholz.

Mountain ecotones, such as the alpine-treeline ecotone, provide a unique opportunity to study plant ecology. The elevational gradient causes changes in temperature, precipitation, and soil composition. As mentioned before, higher elevations of the Rocky Mountains experience lower temperatures and higher precipitation. This gradient directly influences the communities present at each elevation and the traits present within a species. The use of an elevational gradient as a space-for-time substitution can serve as a predictive tool, allowing us to infer potential impacts of climate change over time based on spatial patterns observed across elevations (Blois et al., 2013). Due to the natural environmental gradient, we can expect vegetation of lower elevations to reflect what vegetation after future warming will look like.

Using an elevational gradient allows for studying plant traits and overall community composition within a relatively small spatial area. The change in abiotic conditions allows us to analyze the possible effects of climate change on plant traits and ecology. Using climate change projections in conjunction with field measurements of current vegetation status, we can predict the future of plant traits and the direction of the ecotonal shift of the alpine-treeline ecotone after climate change.

Alpine treeline ecotones have been identified as early-warning monitors of climate change impacts (Camarero et al., 2017). As mentioned before, the high elevations of the Rocky Mountains may also be among the ecosystems most vulnerable to climate change. Several studies have investigated the shift of treeline upslope in the long term. Warming temperatures appear to increase species establishment and stand density of trees (Danby & Hik, 2007; Elliott & Baker, 2004; Hessler & Baker, 1997). While this observation centers on traits associated with sexual reproduction, it exemplifies the spectrum of plant responses to climate change, including those not directly related to clonal growth.

Trait-Based Plant Responses to Environmental Change

Plants, in particular, face heavy pressure to adapt since they have no mechanism for rapid relocation. However, phenotypic plasticity provides a mechanism for plants to respond quickly to their environment (Nicotra et al., 2010), and examining trait variation is one way to understand potential plasticity. The trait-based response-and-effect framework, as discussed by Suding et al. (2008), emphasizes the critical distinction between how plant communities respond to environmental changes (response traits) and how these changes influence ecosystem processes (effect traits). This approach highlights the importance of studying a wide array of plant traits, beyond clonality, to understand the full spectrum of responses to environmental changes. Traits such as leaf size, root architecture, and reproductive timing, along with physiological adaptations like water use efficiency and photosynthetic rates, offer valuable insights into plant strategies for coping with stressors such as drought and temperature extremes. By characterizing these traits across different species and ecosystems, researchers can identify patterns of resilience and vulnerability, shedding light on the strategies plants employ to survive under changing conditions. The trait-based perspective is pivotal for predicting plant community dynamics and ecosystem functions in a warming world (Huxley et al., 2023).

Clonality

Clonality refers to the mechanism by which plants can reproduce asexually or vegetatively to produce a genetically identical ramet, which may remain integrated or fragment from the parent plant. Clonal plants are classified by their clonal growth organs (CGOs), each with a different morphology, tissue of origin, and function. Plants may possess multiple CGOs, which may be additive (providing additional opportunities for persistence and spread), necessary

(the primary means of reproduction), or regenerative (contributing to recovery after disturbance). (Klimešová et al., 2019).

About two-thirds of plant species possess some form of clonal growth (Herben & Klimešová, 2020), emphasizing the importance of studying traits related to clonality in the context of global change. Herben et al. (2015) elaborate on this by comparing clonal growth to sexual reproduction, indicating that clonal plants generally exhibit lower reproductive rates compared to nonclonal species, especially those with extensive lateral spread, which have even lower reproductive outputs.

Traits related to clonal growth influence the distribution, success, and dominance of clonal plants within a community. For example, lateral spread, a trait common to clonality, enables plants to effectively colonize space in habitats with high competition. In studying this, Herben et al. (2016) found no significant relationships between seed reproduction and clonal/bud bank traits, suggesting that these traits are more related to species' roles within the environment.

Integrated ramets may also share resources throughout the entire plant, and thus, ramets in less favorable habitats can persist (Yu et al., 2008). Integration of clonal ramets allows for plants to occupy space and acquire resources in heterogeneous habitats. Another essential trait related to clonality is bud bank size. Buds may be used for seasonal regrowth, branching, flowering, or remain dormant for future use (Klimešová et al., 2019). The collective number of dormant buds on the plant body is called the bud bank. The bud bank is especially important for resprouting after disturbance and to maintain or expand their presence within ecosystems (Qian et al., 2017).

Despite these benefits, traits related to clonality may have tradeoffs in harsh habitats. For example, plants may position rhizomes deep in the soil and litter, insulating them from frost.

However, the deep position may result in delayed emergence and reduced growth due to the energetic cost of a deep rhizome (Lubbe & Henry, 2019). There is a similar energetic cost to maintaining spacers used in lateral spread (Van Groenendael et al., 1996). These findings suggest that in some environments, this energy investment may be a less effective strategy. This idea is further illustrated by studies showing less overall contribution to cover from species that exhibit a high rate of vegetative spread in alpine environments (Evette et al., 2009; Pokarzhevskaya, 1995). A community clonal index found similar results, wherein the lateral spread of the overall community decreases as elevation increases (Rosbakh & Poschlod, 2021). Understanding the benefits and tradeoffs of various clonal traits will help predict future climate change responses and general disturbances. Further, studying the community composition in relation to clonal growth organ, or absence of clonality, helps to illuminate the role of clonality in community dynamics.

In contrast, bud bank size has been observed to increase with elevation (Evette et al., 2009). Additionally, bud bank density increased with decreasing temperatures and increasing precipitation (Qian et al., 2017), such as what we see along the elevational gradient of Colorado. These findings suggest that alpine ecosystems will consist of species that have less lateral spread, but denser bud banks.

The presence of clonality in plant populations often leads to assumptions about reduced genetic diversity in a population due to the asexual nature of clonal reproduction. Asexual reproduction produces a genetically identical individual to the parent plant rather than the recombination seen in sexually reproducing individuals. This uniformity, while advantageous in stable environments, may pose significant risks under rapidly changing climate conditions,

where a lack of genetic diversity could impede the population's ability to adapt and persist (Herben et al., 2015, 2016, 2019).

However, research by Bauert (1996) in arctic and alpine populations of *Polygonum viviparum* reveals that these assumptions may not hold true across all clonal species. Bauert found intermediate to high levels of genetic diversity in *Polygonum viviparum* populations, challenging the notion that clonal reproduction exclusively leads to genetic uniformity. This study suggests that occasional sexual reproduction or mutation within clonal populations can introduce genetic variability, providing a mechanism for adaptation despite predominantly asexual reproductive modes.

Additionally, studies by Diggle (1997) highlight the importance of ecotypic differentiation as a response to environmental heterogeneity. These adaptations allow clonal plants to exploit a range of environments, further contributing to the resilience and adaptability of clonal populations in diverse environments. For instance, Diggle (1997) observed phenotypic plasticity in alpine populations of *Polygonum viviparum*, indicating an ability to adjust growth patterns in response to environmental stressors.

Furthermore, recent studies suggest that clonal plants, through epigenetic modifications, can exhibit a form of adaptive plasticity, enabling them to respond quickly and efficiently to environmental changes without the need for genetic variation (Dodd & Douhovnikoff, 2016; Verhoeven & Preite, 2014). This epigenetic potential could offer an additional mechanism to compensate for the perceived lack of genetic diversity in clonal populations, providing a rapid response to climate change that might not be available through genetic variation alone.

Therefore, while clonality might suggest a constraint on genetic diversity, the capacity for occasional sexual reproduction, mutation, and ecotypic differentiation, not to mention the typical

modular growth, provides a perspective of how these populations can maintain genetic diversity and adapt to changing environments. These findings advocate for integrating a broad spectrum of plant traits, including clonality, in research frameworks aimed at understanding plant responses to climate change. For a comprehensive overview of studies that support these insights, see Table 1.1 below.

Table 1.1*Synthesis of Clonal Growth Research: Traits, Variability, and Trends Across Ecosystems*

Citation and Location of Study	Title	Clonal Traits	Key Findings
<i>Biological Interactions and Reproductive Strategies</i>			
Herben et al. (2015); Central Europe	Clonal growth and sexual reproduction: tradeoffs and environmental constraints	Capacity for clonality, size and depth of bank, connection persistence, multiplication rate, distance of lateral spread	Clonal plants generally have lower reproduction compared to non-clonal plants. Further, species with extensive lateral spread have even lower reproductive output. Reproductive output in clonal and nonclonal plants increases with nutrient and light levels and decreases with moisture. However, in lower quality ecosystems, clonal plants may capitalize on their abilities.
Herben et al. (2016); Central Europe	Reproduction by seed and clonality in plants: correlated syndromes or independent strategies?	Size and depth of bud bank, number of offspring, distance of lateral spread, persistence of connections	There were no significant relationships between seed reproduction traits and clonal/bud bank traits. Clonal and bud bank traits are more closely related to species' niches and role in population dynamics.
Herben et al. (2019); Czech Republic	Two dimensions of demographic differentiation of species in a mountain grassland community: An experimental test	Distance of lateral spread, ramet biomass, shoot life span, persistence of clonal connections, bud bank size	Each axis predicts different components of species' responses to competition: the slow-fast axis predicts short term responses while the dispersal axis predicts long-term responses. The slow-fast axis is associated with commonly used leaf and seed traits, while the dispersal axis is best predicted by lateral spreading distance.
<i>Climate</i>			
Chelli et al. (2019); Italy	Climate is the main driver of clonal and bud bank traits in Italian forest understories	Capacity for clonality, CGO, connection life span, distance of lateral spread, bud protection, bud bank size	Climate, particularly temperature extremes and seasonality, played a major role in clonal and bud bank traits related to space occupancy and resprouting abilities.
Dalgleish and Hartnett (2006); United States	Below-ground bud banks increase along a precipitation gradient of the North American Great Plains: a test of the meristem limitation hypothesis	Bud bank size	Bud banks increase in size along an increasing precipitation gradient.
Ye et al. (2014); China	Clonality-Climate Relationships along Latitudinal Gradient across China: Adaptation of Clonality to Environments	CGO type	Woody clonality showed higher frequency in wet or climatically stable climates, and herbaceous clonality preferred cold, dry, or climatically instable environments.
<i>Community Composition and Regeneration</i>			
Canullo et al. (2011); Italy	Patterns of Clonal Growth Modes Along a Chronosequence of Post-Coppice Forest Regeneration in Beech Forests of Central Italy	CGO	There was no change in the proportion of clonal species along the time recovered. Clonal growth organs showed correlation with stand age or preference for certain regeneration stages.
Duchoslavová and Herben (2020); Germany	Effect of clonal growth form on the relative performance of species in experimental communities over time	CGO type and spread	Growth form had no pronounced effect on the relative performance of species in the first year after sowing. None of the growth forms gained dominance during the first ten years in the communities of the experiment. Species with long rhizomes performed slightly better than other growth forms, but stoloniferous species performed better when the proportion of nonclonals was higher.

Table 1.1 continued

Citation and Location of Study	Title	Clonal Traits	Key Findings
<i>Elevation</i>			
Evette et al. (2009); France	Environmental Constraints Influence Clonal Traits of Herbaceous Plant Communities in an Alpine Massif	Persistence of connection/integration, clonal production, lateral spread rate, bud bank size.	Clonal traits significantly correlated with environmental factors like elevation and duration of snow cover. Different clonal traits were favored in distinct environmental conditions.
Klimeš (2003); India	Life-forms and clonality of vascular plants along an altitudinal gradient in E Ladakh (NW Himalayas)	Capacity for clonality	The highest percentages of clonal plants were found at low and middle altitudes, with a decline at higher altitudes.
Rosbakh and Poschlod (2021); Germany	Plant community persistence strategy is elevation-specific	Longevity, Lateral Spread, Multiplication	In alpine communities, the main persistence strategy was adult longevity, while in lower elevations persistence was achieved by soil seed banks and extended clonal spread.
<i>Habitat Differentiation and Trait Adaptation</i>			
Klimešová and Herben (2015); Czech Republic	Clonal and bud bank traits: patterns across temperate plant communities	Capacity for clonal growth, size and depth of bud bank, connection persistence, distance of lateral spread	Habitat filtering was stronger for bud bank traits than for clonal traits. The distribution of clonal traits was driven by productivity and wetness gradients, indicating diverse environmental adaptations.
Klimešová et al. (2012); Norway	Clonal growth forms in Arctic plants and their habitat preferences: a study from Petuniabukta, Spitsbergen	CGO, distance of lateral spread, proportion of rhizome types	Clonal growth differed by community with nonclonal plants prevailing in early-succession communities and clonal plants prevailed in wetlands. Plants with hypogeogenous rhizomes were less common with increasing stoniness.
Vojtkó et al. (2017); Central Europe	Clonal vs leaf-height-seed (LHS) traits: which are filtered more strongly across habitats?	Root sprouting capacity, depth and size of bud bank, multiplication rate, lateral spread	Clonal and bud bank traits are crucial for habitat differentiation, strongly correlated with environmental gradients.
Weiser et al. (2016); Czech Republic	Root Foraging Performance and Life-History Traits	Capacity for clonality, maximal lateral spread	Clonal plants and those with extensive vegetative growth showed weaker root foraging compared to nonclonal or slow-growing species.
Wellstein and Kuss (2011); Switzerland	Diversity and Frequency of Clonal Traits Along Natural and Land-Use Gradients in Grasslands of the Swiss Alps	CGO type	Rhizomatous species had the highest frequencies in cold, moist and disturbed sites. Soil moisture was more informative than temperature for the presence of clonal species.
<i>Land and Soil Characteristics</i>			
Martínková et al. (2018); Czech Republic	No evidence for nutrient foraging in root-sprouting clonal plants	Lateral Spread, number of ramets, CGO	Plants produced more biomass in a heterogeneous environment than in a homogeneous environment. The number of ramets did not differ between patches in the heterogeneous environment.
Rusch et al. (2011); Norway	Do Clonal and Bud Bank Traits Vary in Correspondence with Soil Properties and Resource Acquisition Strategies? Patterns in Alpine Communities in the Scandian Mountains	Depth and size of bud bank, distance of lateral spread, CGO, persistence of connection	The distributions of CGO composition were significantly associated with soil property variations. Sites with higher lateral spread rates and shorter plant-offspring connection persistence showed increased leaf dry matter content, leaf size, and plant height.

Table 1.1 continued

Citation and Location of Study	Title	Clonal Traits	Key Findings
Conti et al. (2022); Czech Republic, Slovakia, Spain	Insularity promotes plant persistence strategies in edaphic island systems	Size and depth of bud bank, CGO, CGO persistence, distance of lateral spread	Being found on an edaphic island was associated with persistence traits (further lateral spread) and reduced variability in persistence traits.
Halassy et al. (2005); Italy	Patterns of functional clonal traits and clonal growth modes in contrasting grasslands in the central Apennines, Italy	Position of connections, length of spacers, multiplication rate, persistence of connections	There were significant differences in dominant clonal growth modes between mesic and xeric grasslands. Clonality is crucial for coping with water stress.
Zandt et al. (2022); Czech Republic	Plant life history traits rather than soil legacies determine colonization of soil patches in a multi-species grassland	Lateral spread	Fast-spreading, clonal species initially obtained the highest biomass in soil patches. Colonization success was largely determined by the species' reproductive strategy, lateral spread, and growth rate, not the soil patch conditioning species.
<i>Management and Disturbance</i>			
Kermavnar et al. (2021); Slovenia	Effects of disturbance frequency and severity on plant traits: An assessment across a temperate flora	Clonal growth, bud bank	Clonal and bud bank traits' diversity is significantly influenced by climatic signals, contrasting with the sole soil and nutrient influence on leaf-height-seed traits. Both species and trait diversity are primarily controlled by local stand characteristics and soil properties.
Albert et al. (2019); Czech Republic	Grassland restoration on ex-arable land by transfer of brush-harvested propagules and green hay	Lateral Spread	Species with a low capacity for lateral spread were the most successfully harvested and established following restoration utilizing a seed mix.
Benot et al. (2011); France	Spatial patterns in defoliation and the expression of clonal traits in grazed meadows	CGO, above- and below-ground bud bank size, ramet life span, connection life span, clonal multiplication rate, distance of lateral spread	Higher levels of grazing encouraged growth of plants with clonal traits, which help them cope with energetic costs of clonality; aboveground CGOs, short distance lateral spread, and short-lived connections. In ungrazed conditions, plants with clonal traits that give them a competitive edge were favored.
Herben et al. (2018); Central Europe	Effects of disturbance frequency and severity on plant traits: An assessment across a temperate flora	CGO, bud bank size	Clonal growth form and bud bank size exhibit a unimodal response to disturbance frequency. Clonal growth shows a stronger relationship to environmental conditions than leaf-height-seed traits.
Świerszcz et al. (2019); Poland	Varied response of underground and aboveground plant matter: functional diversity of three different vegetational types after translocation to reclaimed postindustrial land	Depth and size of bud bank, distance of lateral spread	In meadow habitats, there was a significant increase in community weighted means for bud bank size, bud bank depth, and lateral spread. In dry heath, the community weighted means of bud bank depth increased, and lateral spread decreased.

Our comprehensive investigation into the clonal growth patterns and intraspecific trait variation across the elevational gradient in the Colorado Front Range illustrates the importance of considering clonality in predictive plant ecology. This review highlights the adaptive significance of clonal strategies, such as lateral spread and bud bank size, for surviving in alpine environments.

Building on the insights observed here, several pathways for future research emerge. The dynamics of clonal trait variation under climate stressors necessitate long-term observational studies to capture the ecological responses of clonal species. Additionally, the genetic factors associated with clonality, and their interactions with environmental factors, present further opportunities for future research. Exploring the balance between clonal and sexual reproduction in plant populations across different environmental gradients could provide deeper insights into the resilience and adaptability of these species. Moreover, examining the role of epigenetic mechanisms in clonal adaptation offers a promising avenue for understanding how clonal plants might rapidly adjust to environmental changes without genetic variation.

The forthcoming chapter is a vital contribution to our knowledge of vegetation community dynamics under climate change. By studying the role of clonal traits within the Colorado Front Range's elevational gradient, our work shows the strategies employed by alpine plants to survive in a changing climate. Furthermore, this research highlights the need for a multidimensional approach for studying plant ecology, one that incorporates clonal growth patterns, genetic diversity, and trait plasticity. Such an approach is essential for developing effective conservation strategies and predictive models that account for the dynamic responses of plant communities to global climate change.

CHAPTER II

EFFECTS OF ELEVATION AND ECOSYSTEM ON CLONAL GROWTH PATTERNS AND INTRASPECIFIC TRAIT VARIATION IN THE COLORADO FRONT RANGE

Contribution of Authors and Co-Authors

Manuscript in Chapter II

Author: Jordan N. Conley

Contributions: Conceived the study topic, developed and implemented the study design. Generated and analyzed data. Wrote first draft of the manuscript.

Co-Author: Dr. Scott Franklin

Contributions: Helped conceive the study design. Provided feedback on statistical analyses and early drafts of the manuscript.

Co-Author: Dr. Mit McGlaughlin

Contributions: Provided expertise regarding field methods. Provided feedback and comments on the manuscript.

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Contributions: Provided feedback on the study design. Provided feedback and comments on the manuscript.

Abstract

In the face of global climate change, understanding the adaptive strategies of alpine flora is crucial for predicting and managing future biodiversity. This study investigates the clonal growth patterns and intraspecific trait variation of plants across an elevational gradient in the Colorado Front Range, within the Roosevelt National Forest. We collected vegetation cover data from nine sites across three distinct ecosystem types: alpine, ecotone, and forest. This aimed to understand the dominance and distribution of clonal species. By focusing on two species with varying clonal growth organs (CGOs), we analyzed trait data including lateral spread, number of buds, and number of bulbils. Permutational Multivariate Analysis of Variance (PerMANOVA) and Multi-Response Permutation Procedures (MRPP) were used to assess community composition, while species richness and diversity indices were calculated to evaluate biodiversity. We found significant effects of ecosystem type on community composition. This was further supported by an indicator species analysis and diversity measures. When performing the PerMANOVA for species capable of clonal growth, we saw a significant difference among ecosystem types, with alpine and forest ecosystems exhibiting increased dominance. Finally, intraspecific trait variation was analyzed for two species. Welch two-sample t-tests found no significant differences in number of buds or distance of lateral spread of *Carex nardina*, or number of buds of *Polygonum viviparum*. However, we observed trends that may suggest clonal trait variation within species. The study offers novel insights into the complex adaptive strategies of clonal plants in alpine ecosystems, highlighting their potential resilience to climatic shifts and contributing valuable data for conservation efforts.

Introduction

Despite about two-thirds of plant species possessing some form of clonal growth (Herben & Klimešová, 2020), many studies fail to account for the possible advantages and disadvantages of clonality. This oversight could have significant implications for ecological predictions in changing climates, where the risks and benefits associated with utilizing clonal growth play crucial roles. Here, we examine Rocky Mountain alpine ecosystems, where the effects of climate change present unique challenges. The varied elevations can reveal how clonality influences plant dominance and fitness in response to changing climates. Climate change models have projected a warming trend for the Rocky Mountain alpine ecosystems, with studies noting significant temperature increases (Diaz & Eischeid, 2007; Fyfe & Flato, 1999; Snyder et al., 2002). This warming has led to earlier snowmelt in high-elevation ecosystems, which could escalate the risk of frost injury to plant tissues due to the exposure to late-season frosts after premature snowmelt (Preston et al., 2016). The varying altitudes of mountains, therefore, offer a gradient through which we can assess the resilience of clonal strategies under these emerging conditions. The resilience of clonal plants in these ecosystems may be a key indicator of broader ecological responses to global warming, prompting our investigation into the dominance of clonality along the gradient and the collection of critical trait data from the Rocky Mountain alpine ecosystems, an area where such data are scarce. By examining how clonal growth traits change across elevations, and thus ecosystems, we aim to elucidate the nuanced ways that clonal plants adapt to and potentially thrive in varying environmental conditions. This approach helps explain the complex interplay between clonal growth forms and their ecological contexts,

informing our hypotheses about clonality's role in plant survival and competitive dynamics under shifting climatic conditions.

In this study, we define clonal growth as the mechanism by which plants can reproduce vegetatively. This results in a genetically identical new individual called a ramet, which may remain integrated or fragment from the parent plant. However, not all clonal plants are the same. Clonal growth organs (CGOs) are a way to classify clonal plants. Each CGO has a unique morphology, tissue of origin, and function. Plants may possess more than one CGO, with each being further classified as necessary, additive, or regenerative (Klimešová et al., 2019). Clonal plants can also exhibit related traits that provide advantages in various ecological situations. These characteristics are crucial for understanding clonal plants' ecological roles.

To further understand the resilience of clonal plants under variable conditions, the plasticity of clonal traits becomes a critical focus. For example, clonal plants that possess rhizomes often position their rhizomes deep in the soil or under litter, though this could cause delayed emergence or reduced growth (Lubbe & Henry, 2019). While beneficial for frost protection, this trait may need to be balanced against the potential for reduced reproductive success in a warmer climate. Moreover, regardless of the tradeoffs related to clonality, the mechanism could allow an individual (i.e., ramets) to share resources across the whole individual (i.e., genet). Clonal propagation allows a new ramet to bypass the vulnerable seedling stage, relying on the parent plant for nutrient uptake until establishment occurs. This is facilitated by physiological integration, which allows plants to share resources – like water, nutrients, and carbohydrates - across different parts of the individual, allowing them to survive even in resource-poor microhabitats. A meta-analysis found that, overall, physiological integration

increased the growth of whole clones in both homogenous and heterogenous environments (Wang et al., 2021).

The adaptability of clonal plants is further manifested in their reproductive strategies. The balance between sexual and asexual reproduction in clonal plants may shift to optimize survival and reproduction, emphasizing clonality's adaptability in response to environmental changes (Hessl & Baker, 1997). The availability of resources, which can vary significantly with elevation, often dictates plant growth patterns, leading to diverse forms of plant architecture and reproduction strategies (Preston et al., 2016). Additionally, interactions with other species and the plants' inherent stress tolerance mechanisms are also likely to influence trait expression across an elevational gradient.

Recent studies, such as Ding et al., (2019), have demonstrated that in alpine meadows on the Zoige Plateau, an increase in temperature led to a higher total number of belowground buds, suggesting a potential shift in clonal growth trait expression with altitude. Clonal traits in plants, which are subject to variation with elevation, are a crucial component of their survival and reproductive strategies (Diaz & Eischeid, 2007; Fyfe & Flato, 1999).

Traits related to clonality influence species' dominance, distribution, and overall fitness within a plant community. By studying these traits across the environmental gradient of a mountain, we can gain insights into the broader patterns of adaptation and survival. The ability of clonal plants to dominate certain environments may be crucial in the face of these climatic shifts. Thus, mountains provide a critical setting to explore how clonal plants might restructure community composition and express intraspecific variation in response to climate gradients. For one, dominant plant genotypes in a community must be highly adapted to the environment in which they are found and can outcompete other individuals. In addition, clonal plants' longevity

allows them to survive across climate oscillations, with some species living for centuries. Several European arctic-alpine species have been estimated to have genets at least 450 years old, up to an estimated 4100-5000 years old for one species, indicating that these individuals survived climate oscillations such as post-industrial warming (De Witte et al., 2012). The diverse microclimates of mountain slopes will allow us to observe these adaptations first-hand.

Warmer temperatures may facilitate the upward migration of species from lower elevations (Danby & Hik, 2007; Elliott & Baker, 2004; Hessel & Baker, 1997), intensifying competition among native and ascending species and potentially leading to the loss of suitable habitats for cold-adapted alpine flora. Mountains represent the complexity of these dynamics in a small spatial area, allowing for observation of clonal plants' adaptive strategies. These shifts highlight the adaptive significance of clonality in alpine ecosystems.

The adaptability of clonal plants suggests that in ecotonal areas – the transitional zones between two ecosystems – clonality may not necessarily be the dominant survival strategy. Evidence from Silvertown (2008) indicates that clonality increases with population age, suggesting that disturbance disrupts clonal growth. When disturbances were frequent and site productivity was low, resprouters were outcompeted by short-lived seeding plants (Bellingham & Sparrow, 2003). These findings were tested in similar conditions found in the alpine-forest ecotone, which may be less insulated by snow compared to alpine zones, exposing them to harsher freeze-thaw cycles and reducing the protective benefits of a consistent snowpack. The harsh and fluctuating conditions of ecotones challenge the traditional advantages of clonality, suggesting that in these transitional zones, the strategy may become less dominant. The observation of an increased frequency of clones at the geographical margins (Silvertown, 2008) further complicates the situation, suggesting that while clonality serves as a mechanism for

persistence and colonization at the edges of a species' tolerable range, the unique stresses of ecotones – including disturbance and competition from adjacent ecosystems – may diminish clonality's dominance as a survival strategy within these transition areas.

Our research will investigate how these traits vary in the scale of a mountain environment, providing context for predictions of future ecological shifts across larger landscapes. Our intention is to illuminate how clonal plants adapt across a gradient that is under pressure from climate change, providing critical insight into conservation efforts. By addressing these pressing questions, this study aims to explore the patterns of dominance and distributions among clonal species across environmental gradients in the Colorado Front Range, employing a trait-based comparative analysis to understand the adaptive strategies of alpine flora and their implications for conservation amid rapid climate change. The study investigates the following research questions and hypotheses.

Research Questions

- Q1 How does plant dominance change across the environmental gradient?
- Q2 How does clonal dominance change across the environmental gradient?
- Q3 How does intraspecific clonal trait variation change across the environmental gradient?

Hypotheses

- H1 There will be a change in community composition across the gradient.
- H2 In alpine and forest ecosystems, clonal plants will be dominant in cover.
- H3 Clonal plants exhibit significant intraspecific trait variation across environmental gradients.

Methods

Study Area

Study area elevations ranged from 3200 to 3450 meters above sea level (m a.s.l.) within the Colorado Front Range, situated within Roosevelt National Forest. The region experiences a diverse range of ecological conditions, characterized by variations in mean annual temperature and precipitation patterns. This diverse range of conditions within a compact geographical area makes mountains ideal natural laboratories. Specifically, they serve as space-for-time substitutions, offering a unique opportunity to study plant trait responses to climatic changes across different elevations.

Study Sites

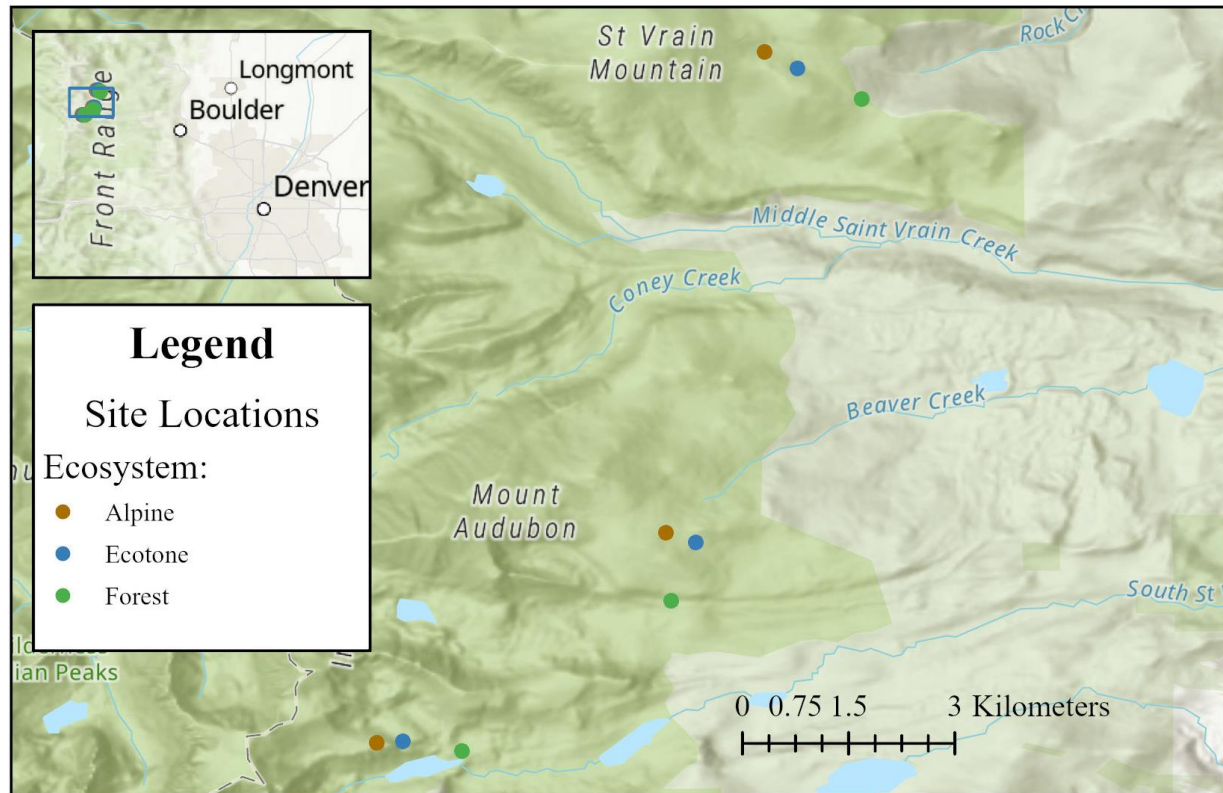
Study Sites were chosen based on several criteria to ensure consistency and accessibility for the study. Each site was chosen to have a northern exposure (between 41 and 174 degrees) to minimize variations in sunlight and temperature that could influence plant growth. Additionally, we chose mountains that had a minimum peak elevation of 3,700 m, to ensure adequate representation of the ecotone and alpine ecosystems. Accessibility was also a key factor. All sites were reachable by foot, but they were situated along less frequented trails to minimize human impacts.

Vegetation cover data were gathered from nine distinct sites, with each site representing one of three ecosystem types – alpine, ecotone, and forest (Figure 2.1). To capture the full spectrum of ecological diversity within these categories, the distance between the furthest sites was 10.598 km, aiming to reduce spatial distance as a factor in variability. This strategic selection of sites enhances the robustness of our data, allowing for a more comprehensive

analysis of vegetation dynamics across these distinct ecosystems. On each mountain, the alpine plot was established first. This systematic approach ensured that our sampling accurately reflected the elevation gradient. We then moved downward in elevation, attempting to find an ecotone (krummholz) site within 25-125 m lower than the previous elevation as measured by a Garmin GPS, and then the same for the forest site. In some cases, the hillside's topography and exposure affected the change rate from one vegetation type to another. As mentioned before, vegetation characteristics were considered due to the study's goal of relating trait presence and ecosystem type. We recorded GPS coordinates, elevation, and slope aspects at each site. The elevation and slope aspect were later verified in ArcGIS due to the error associated with field instruments. Plots were established following the Carolina Vegetation Survey (CVS) protocol to ensure reliability and randomization of our sampling method. This involved the creation of a 0.1 ha (20 by 50 m) plot divided into ten modules (Peet et al., 2018). One 50-meter tape was run along the slope contour, serving as the midline of the plots. A 15-meter tape was run from this midline tape to either side of the plot to estimate the percentage cover for each corner. From these modules, four were selected for intensive sampling following the diagram presented in the CVS protocol. In these four plots, two one m² corner subplots were selected (total of eight subplots). Each one m² subplot was sampled for species percent cover. This included the herbaceous strata, and not trees unless they were young and were at the level of the herbaceous strata. Cover data were visually estimated for each species within the corners sampled, and subplots averaged at the plot scale for analyses. Species outside the intensively sampled corners but inside the plot were recorded as residual. Unknown species were collected or photographed for later identification with dichotomous keys. A total of 64 species were included in the dataset.

Figure 2.1

Map of Sampling Sites by Ecosystem Type in the Roosevelt National Forest



Species Selection for Trait Analysis

Species selection for trait analysis was informed by the vegetation cover data collected from alpine and ecotone sites across three peaks, ensuring the representation of species within most of the study plots. We focused on three functional types: shrub, forb, and sedge, crucial for understanding the diverse clonal strategies within these ecosystems (Table 2.1).

Table 2.1

Species Selected for Trait Analysis, Growth Form, Dominant Clonal Growth Organ, and Other Clonal Growth Organs Observed

Species	Growth Form	Dominant Clonal Growth Organ	Other Clonal Growth Organs Observed
<i>Salix glauca</i>	Shrub	Nonclonal	Rhizome
<i>Polygonum viviparum</i>	Forb	Rhizome	Bulbils
<i>Carex nardina</i>	Sedge	Rhizome	

For each selected species, 3-5 individuals were collected from each alpine and ecotone site, ensuring comprehensive sampling across the plot. In instances where fewer than three individuals were found, additional samples were collected within a 50-meter radius of the plot. This approach was used to account for potential rhizome or stolon connections leading to other ramets. Sedge and forb samples were preserved at 4°C after collection.

To avoid the inadvertent collection of clonal individuals among shrubs, a minimum distance of 10 meters was maintained between each sampled individual. This was facilitated by marking the soil level of each sample with flagging tape and carefully excavating the surrounding area to access belowground tissues. Only terminal branches, at least 20 cm in length, were collected to standardize the sampling method, with all samples subsequently stored in paper bags at room temperature.

Assignment to Clonal/Nonclonal and Clonal Growth Organ

Clonal trait data were obtained from the CLO-PLA3 database (Klimešová & Klimeš, n.d.) for eight species. Since the database focuses on Central European flora, most of the species in our study sites were absent. From the TRY Database (Kattge et al., 2020), we were able to incorporate further trait data by species. The remaining species were assigned based on a literature search and examination of herbarium specimens.

Species were first assigned to two groups: Clonal or Nonclonal. We referenced CLO-PLA3 (Klimešová & Klimeš, n.d.) and TRY Databases first (Kattge et al., 2020). We then referenced literature including the name of each species, searching for words that may be related to clonal growth (rhizome, stolon, vegetative spread, etc.). If no evidence of asexual reproduction or mention of rhizomes or stolons was found, the species was categorized as Nonclonal. Therefore, this attribute is evaluating the ability of the species to utilize clonal growth, disregarding the actual rate of clonal growth.

Instead of categorizing species into the 17 CGOs that CLO-PLA identifies, we categorized them into three categories: rhizomes, stolons, and nonclonal. This was due to several factors; (1) the CGO was absent from our data set and (2) literature descriptions referred to them as rhizomes or stolons and did not provide enough context to categorize them further. Specifically, hypogeogenous rhizomes and epigeogenous rhizomes were combined into one category. We also considered Rooting horizontal stems at or above soil surface analogous to stolons.

Trait Measurements

Traits of interest included lateral spread, number of buds, and number of bulbils were measured following the comprehensive protocols outlined in the ‘Handbook of standardized protocols for collecting plant modularity traits’ by Klimešová et al. (2019), illustrated in Figure 2.2. Lateral spread was measured by identifying the ramets and measuring the distance between them with a digital caliper. Since it was difficult to assess which ramets were from the current year, and which were from the previous year, we took the mean for each individual. The number of buds were counted under a dissecting microscope and then divided by the number of rooting units forming a clonal fragment, regardless of length as detailed by Klimešová et al. (2019). In

the case of *Polygonum viviparum*, there were no offspring ramets, so buds were counted per individual. Finally, the number of bulbils were counted after being removed from the plant.

Figure 2.2

Clonal Traits of Interest in Species of Interest



Notes. A.) Rhizomes of *Carex nardina*. Lateral spread was measured between ramets. Bulbils of *Polygonum viviparum* B.) removed from the plant (under microscope) and C.) on stalk.

Data Analysis

Non-Metric Multidimensional Scaling (NMDS)

Non-Metric Multidimensional Scaling (NMDS) was applied to visualize the community composition data, using the “metaMDS” function in the *vegan* package (Oksanen et al., 2022) of R 4.3.1 (R Core Team, 2023), with a Bray-Curtis dissimilarity matrix. This ordination method allowed for the exploration of patterns in species composition across different site types, with stress values calculated to assess the goodness of fit. Following a visual separation of the site types, we performed further analysis.

Following ordination visualization, an indicator species analysis was used to identify species with strong associations to specific ecosystem types, utilizing the *indicspecies* package (De Cáceres & Legendre, 2009) in R. This analysis identifies species that demonstrate high fidelity and specificity to their respective ecosystem types.

Community Composition Analysis

We first performed correlation analyses to remove highly correlated variables. We first utilized Spearman correlations to exclude numerical variables, using an R^2 threshold of 0.9 for the correlation coefficient, such as removing El_GPS (elevation obtained from GPS) and retaining El_GIS (elevation verified by GIS). We then performed ANOVAs to assess correlation between categorical variables such as mountain (Mt) and ecosystem (ES). After obtaining R^2 values, we excluded Latitude (Lat) and Longitude (Lng), retaining mountain (Mt), and El_GIS, retaining ecosystem (ES). While latitude and longitude met the R^2 threshold of 0.9, elevation did not. However, due to the closeness of the R^2 value (0.8757577), and the knowledge that ecosystems vary by elevation, we excluded elevation too.

To investigate the effects of environmental variables on community composition (Hypothesis 1), we utilized Permutational Multivariate Analysis of Variance (PerMANOVA) using the *vegan* package (Oksanen et al., 2022). This was executed focusing on the main effects of ecosystem type, aspect, slope, and elevation to further elucidate their specific contributions to community composition variations.

Species Richness and Diversity Indices

Species richness and Shannon diversity indices were calculated for each site type (alpine, ecotone, forest) to assess biodiversity and competition at each of the sites (Hypothesis 1). Species richness was determined as the total number of species present in each site, while Shannon diversity indices were calculated to evaluate the combined diversity and evenness of species. The Shapiro-Wilk test was employed to verify the normality of the data for richness of alpine ($p = 1.00$), ecotone ($p = 0.637$), and forest ($p = 0.780$). The Shapiro-Wilk normality test was also applied to the Shannon diversity data, yielding a W-statistic of 0.89102 with an associated p-value of 0.2044. The Shapiro-Wilk normality test for evenness yielded a W statistic of 0.95791 and a p-value of 0.7763. These were followed by ANOVA and Tukey's Honest Significant Difference (HSD) post hoc tests to compare species richness and diversity across site types. The Shapiro-Wilk normality test for life form abundance indicated non-normality (alpine, $p = 0.07916$; ecotone, $p = 0.1903$; forest, $p = 0.0004503$). Life form abundances within communities were analyzed using Kruskal-Wallis rank sum tests due to non-normal distributions of the data. These non-parametric tests assessed differences in the total abundance of different life forms across alpine, ecotone, and forest ecosystems, again informing us of the potential competition encountered within the sites (Hypothesis 1).

Clonality and Dominant Clonal Growth Organ Analysis

To assess the impact of various environmental factors on the abundance of species capable of clonality within a community (Hypothesis 2), an additional PerMANOVA was performed, utilizing the same explanatory variables as in the previous model (ecosystem, aspect, slope, and mountain).

We then assessed the presence of clonal versus non-clonal species across different site (ecosystem) types. We first calculated the richness of clonal versus nonclonal species and then calculated the proportion of each for the different ecosystems: alpine, ecotone, and forest. The Shapiro-Wilk test for normality yielded a W-statistic of 0.95323 and p-value of 0.7255, suggesting that parametric methods are appropriate. A one-way ANOVA was conducted to detect significant differences in the proportion of species capable of clonality among the site types. This was followed by Tukey's HSD post-hoc test to assess pairwise differences between site types.

We then performed analysis on the dominant clonal growth organ of each species. Shapiro-Wilk tests on arcsine-transformed proportions for alpine, ecotone, and forest site types all indicate significant deviations from normality (p-values: alpine = 0.006295, ecotone = 0.00304, forest = 0.01812), suggesting the need for non-parametric methods in subsequent analysis. The Kruskal-Wallis rank sum test was utilized to analyze the arcsine-transformed proportions of dominant CGO among site types.

Clonal Trait Analysis

For specific species, clonal traits such as the number of buds per rooting unit, number of bulbils, and mean lateral spread were analyzed to understand clonal strategies across different habitats (Hypothesis 3).

To assess the distribution of clonal traits across the different habitat types, we initially conducted Shapiro-Wilk tests for normality on the mean numbers of buds in *Polygonum viviparum*. The test for mean buds yielded a W statistic of 0.94219 with a p-value of 0.6769, suggesting that parametric tests are appropriate. Since only one individual had bulbils, we did not analyze further. The Shapiro-Wilk normality tests for *Carex nardina* was performed to assess the distribution of these traits, with results indicating that both mean buds per rooting unit (p-value = 0.6436) and mean lateral spread (p-value = 0.1954) do not significantly deviate from a normal distribution. These findings supported the use of a Two-Sample t-test for comparing trait distributions between habitat types.

Results

Nonmetric Multidimensional Scaling (NMDS) and Indicator Species Analysis

The NMDS analysis, with a low stress value of 0.0786, suggests a good fit and reveals clear distinctions in species composition across different site types (Figure 2.3). Forest sites are dispersed from the alpine and ecotone sites along NMDS Axis 1. Axis 2 further separates alpine and ecotone sites.

After visualizing distinctions among ecosystem types, an indicator species analysis revealed specific species associations to ecosystem types (Table 2.2). Among the 64 species examined, 10 were significant indicators of distinct associations. Of these, eight species were associated with one ecosystem type, while two species were associated with two ecosystem groups. The analysis also provided values for specificity, if the species occurs only in that group, and fidelity, how consistently or frequently a species occurs in the ecosystem. In the alpine ecosystem, *Elymus scribneri* emerged as a significant indicator species, with high specificity and fidelity (A=1, B=1, p=0.036). In the ecotone, species included *Castilleja puberula*, *Elymus*

trachycaulus, *Potentilla pulcherrima*, *Antennaria media*, and *Carex elynoides*, each displaying strong fidelity (B=1) and notable specificity (A ranging from 0.846 to 0.9987), with significant p-values (p=0.041). Forest ecosystems exhibited associations with *Abies lasiocarpa* and *Vaccinium cespitosum*, both demonstrating high fidelity and specificity (A=0.9652 to 0.9857, B=1, and p=0.041). Additionally, the alpine and ecotone grouping revealed *Geum rossii* and *Minuartia obtusiloba* as indicator species, with high specificity and fidelity (A=1, B=1, p=0.036). These indicator species were plotted on the NMDS ordination (Figure 2.3), appearing clustered around their respective site types, with the species found in the alpine-ecotone grouping settling in between the two site types, as expected. So, axis 1 of the ordination separates alpine and ecotone from forest, and axis 2 separates alpine and ecotone.

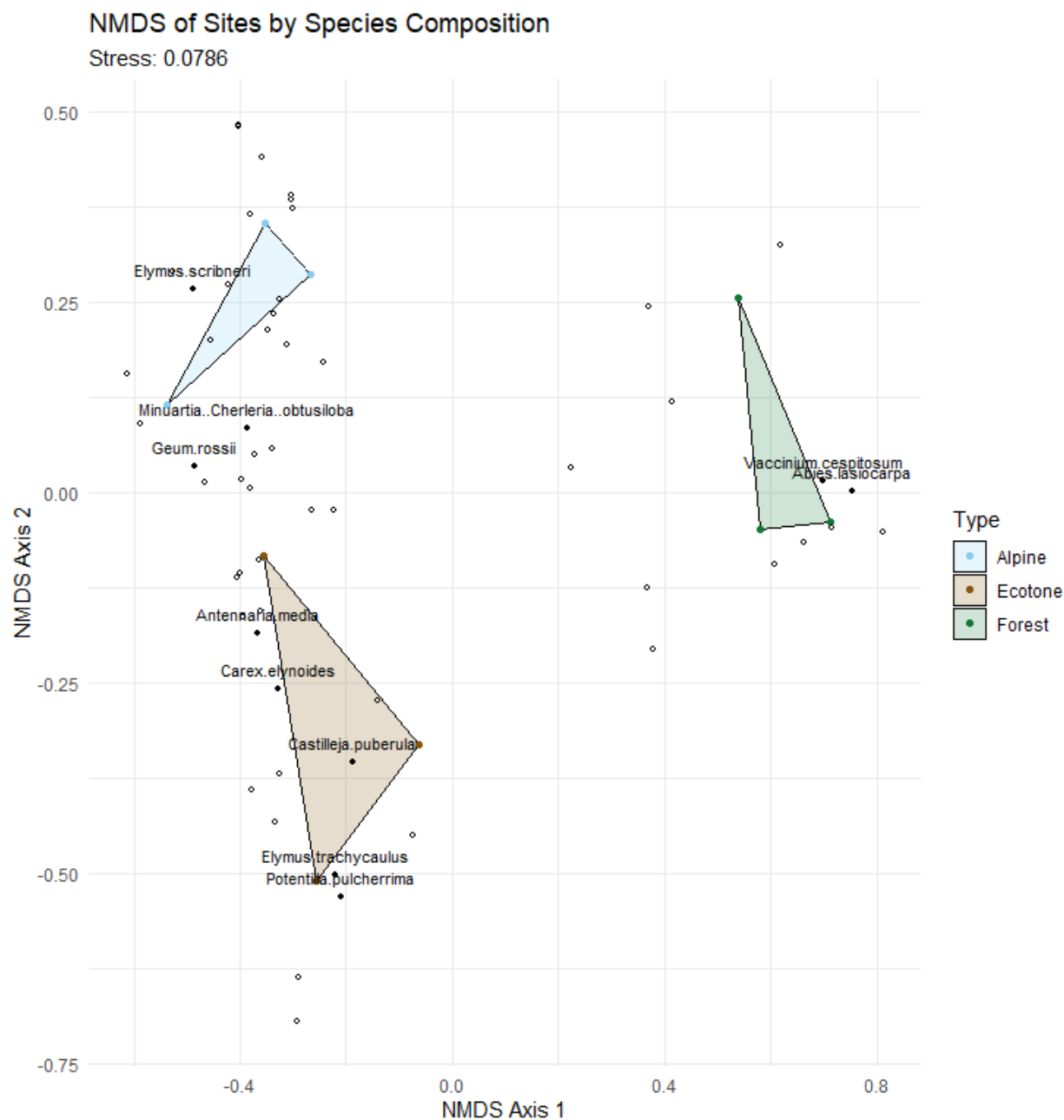
Table 2.2*Indicator Species Analysis Results for Alpine, Ecotone, and Forest Ecosystems*

	A (specificity)	B (fidelity)	stat	p value
Group 1 (Alpine)				
<i>Elymus scribneri</i>	1.0000	1.0000	1.0000	0.036 *
Group 2 (Ecotone)				
<i>Castilleja puberula</i>	0.9987	1.0000	0.999	0.041*
<i>Elymus trachycaulus</i>	0.9977	1.0000	0.999	0.041*
<i>Potentilla pulcherrima</i>	0.9965	1.0000	0.998	0.041*
<i>Antennaria media</i>	0.9811	1.0000	0.991	0.041*
<i>Carex elynoides</i>	0.8462	1.0000	0.920	0.041*
Group 3 (Forest)				
<i>Abies lasiocarpa</i>	0.9857	1.0000	0.993	0.036*
<i>Vaccinium cespitosum</i>	0.9652	1.0000	0.982	0.036*
Group 1 + 2 (Alpine + Ecotone)				
<i>Geum rossii</i>	1.0000	1.0000	1.0000	0.036*
<i>Minuartia obtusiloba</i>	1.0000	1.0000	1.0000	0.036*

Notes. Indicator species analysis including specificity and fidelity across alpine, ecotone, and forest groups. Specificity (A) measures the probability of a site being from a particular group given the presence of the species, indicating the degree to which a species is exclusive to a particular group. Fidelity (B) represents the probability of finding a species in its indicated group, reflecting how consistently a species occurs within that group.

Figure 2.3

Non-Metric Multidimensional Scaling (NMDS) Analysis of Alpine, Ecotone, and Forest Ecosystems Based on Species Composition



Notes. NMDS ordination plot illustrating the differences in species composition among alpine, ecotone, and forest ecosystems. Each black point represents a species, and the colored points represent their respective ecosystem types. The indicator species are included as text.

Community Composition Analysis

We first used PerMANOVA to assess the influence of various environmental variables on community composition (Table 2.3). The PerMANOVA assessed the main effects of ecosystem type, aspect, slope, and elevation on community composition. In this model, only ecosystem type exhibited a significant effect ($F = 7.903$, $R^2 = 0.73408$, $p = 0.010$) on community composition supporting hypothesis 1. No significant differences were observed for other environmental variables such as slope (Slp), slope aspect (Asp), or latitude, longitude, or mountain.

Table 2.3

Impact of Environmental Variables on Community Composition: Permutational Multivariate Analysis of Variance (PerMANOVA) Results

Overall Model					
	Df	SumOfSqs	R ²	F	Pr(>F)
ES	2	0.61972	0.73408	7.9030	0.010**
Asp	1	0.03289	0.03896	0.8389	0.539
Slp	1	0.03685	0.04365	0.9398	0.489
Mt	2	0.07634	0.09043	0.9735	0.544
Residual	2	0.07852	0.09289		
Total	8	0.84422	1.00000		

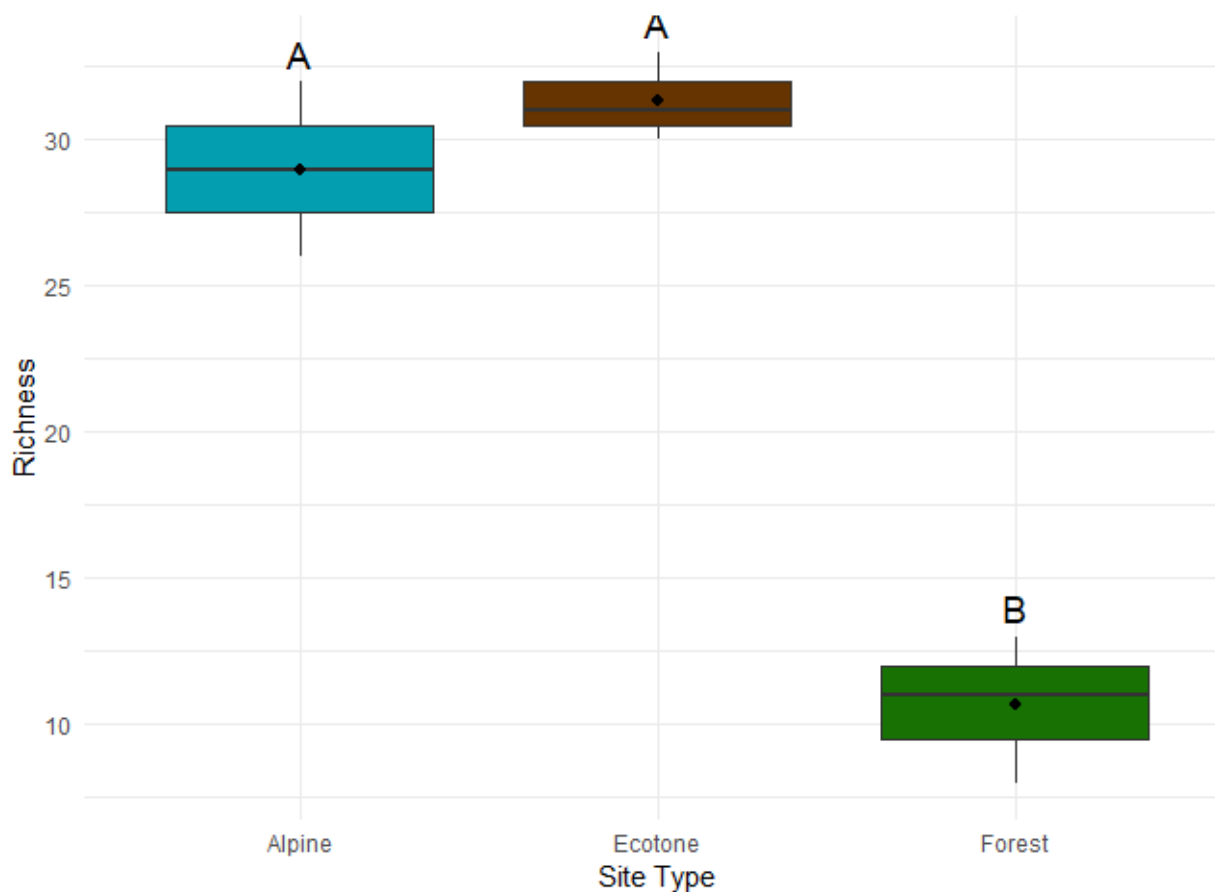
Notes. Environmental variables tested included ecosystem (ES), slope-aspect (Asp), slope (Slp), and mountain (Mt). This analyzed differences in overall community composition by cover in relation to environmental variables.

Richness

Species richness, a measure of the number of different species present in each site, varied significantly among the three site types in the study (Figure 2.4). Alpine sites displayed a high species richness with counts of 33, 27, and 30 species, suggesting that there may be less competition due to the harsh climate. Ecotone sites were comparable in richness, with species counts of 31, 32, and 34. This may be due to a balance between competition (from bordering ecosystems) and varied microhabitats. However, forest sites had markedly lower species richness

than ecotone and alpine, with 9, 14, and 12 species respectively, hinting at potential higher competition levels in the ecotone.

The analysis of variance (ANOVA) on species richness confirmed significant differences across site types ($F(2, 6) = 65.26, p < 0.0001$). Post hoc analysis using Tukey's Honest Significant Difference (HSD) revealed no significant difference in species richness between alpine and ecotone sites (mean difference = 2.333, $p = 0.507$). This suggests that the transition from alpine to ecotone does not significantly affect the number of species present. However, when comparing forest sites to both alpine (mean difference = -18.333, $p = 0.00022$) and ecotone sites (mean difference = -20.667, $p = 0.00011$), there were significant reductions in species richness. These differences were significant, indicating that forest sites have substantially fewer species compared to both alpine and ecotone sites. The lack of significant difference in species richness between alpine and ecotone sites suggests that the gradient does not drastically alter capacity for species diversity. However, this does not inform us of the composition of the sites.

Figure 2.4*Boxplot of Species Richness by Site Type*

Notes. The richness is shown for Alpine, Ecotone, and Forest site types. Means are plotted as points, and medians as bold lines. Letters indicate grouping based on Tukey's post-hoc test, where groups that share a letter are not significantly different ($p > 0.05$), and those with different letters are (Alpine and Ecotone, $p = 0.507$; Forest and Alpine, $p = 0.00022$; Forest and Ecotone, $p = 0.00011$). The overall ANOVA showed a significant effect of Site Type on Species Richness ($F(2,6) = 65.26$, $p < 0.001$).

Shannon Diversity

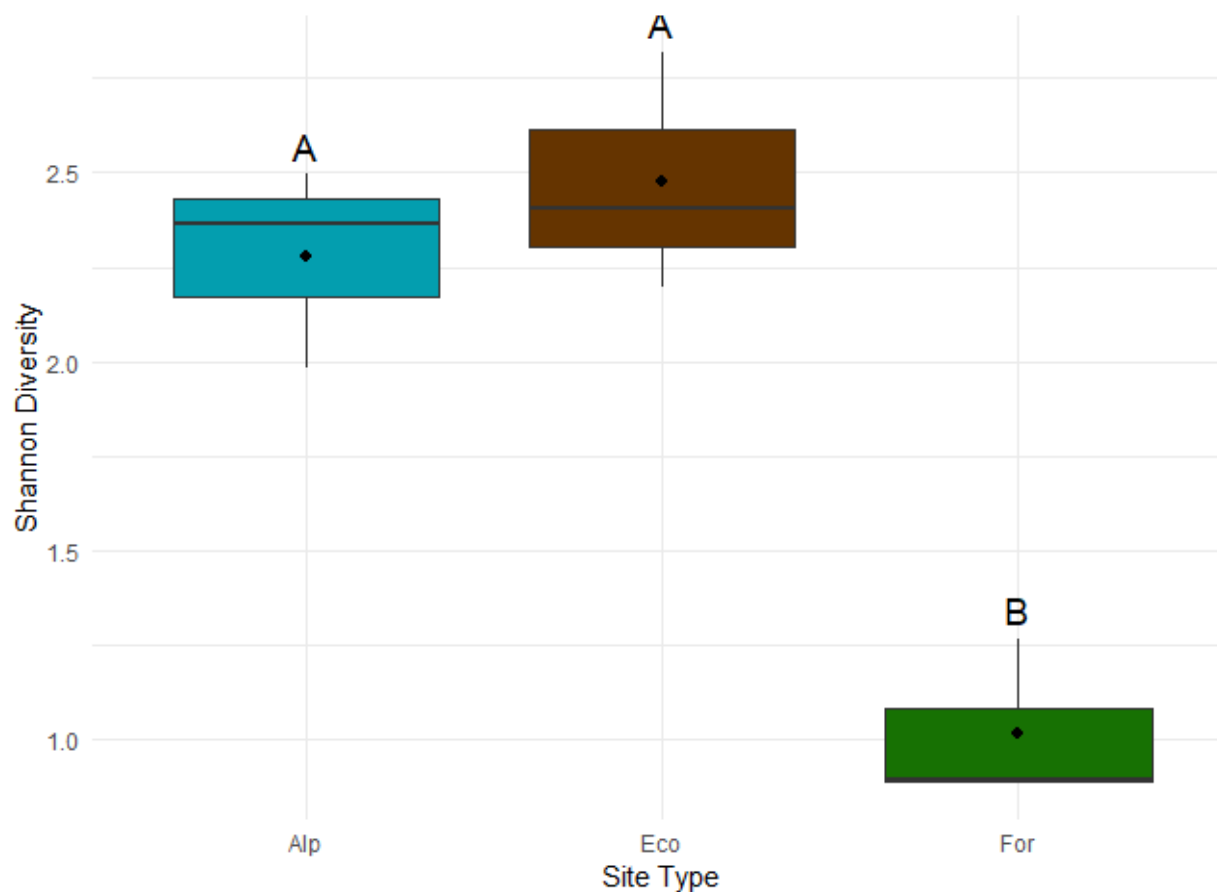
The Shannon diversity index offers insight into the biodiversity present across different site types, revealing variations that may influence community dynamics and competitive interactions among species, including those capable of clonal growth. In this study, the alpine sites exhibited a mean diversity score of 2.17 indicating moderate species diversity (Figure 2.5).

This diversity reflects the harsh, but relatively consistent environment of alpine ecosystems, which can support many highly adapted species.

Ecotone sites demonstrated a slightly higher mean Shannon diversity index of 2.39, suggesting greater biodiversity than observed in alpine sites, possibly due to the transitional nature of these habitats in which species of both ecosystems are present. This increased diversity could result in increased competition due to the greater number of species competing for similar resources.

Contrastingly, forest sites showed a notably lower mean Shannon diversity index of 0.949, suggesting a lower level of biodiversity. This suggests that it could be a more homogeneous environment or dominance of a few species, potentially limiting the opportunities for clonal plants to exploit varied niches and compete effectively.

A one-way ANOVA revealed significant differences in Shannon diversity indices among the three site types ($F(2, 6) = 21.93, p = 0.00174$). Post hoc comparisons using Tukey's Honest Significant Difference (HSD) test indicated no significant difference in biodiversity between ecotone and alpine sites (mean difference = 0.215, $p = 0.650$). However, significant differences were detected when comparing forest sites to both alpine (mean difference = -1.225, $p = 0.0047$) and ecotone sites (mean difference = -1.440, $p = 0.0021$). These findings support the hypothesis that community composition changes across different ecosystem types.

Figure 2.5*Shannon Diversity by Site Type*

Notes. Boxplot comparing Shannon diversity indices across alpine, ecotone, and forest site types. Means are plotted as points, and medians as bold lines. Alpine and Ecotone sites did not show a significant difference in biodiversity ($p = 0.650$), sharing the same Tukey's post-hoc group A. Forest sites exhibited significantly lower diversity compared to both alpine ($p = 0.0047$) and ecotone ($p = 0.0021$) sites. The overall ANOVA confirmed significant differences among the site types ($F(2, 6) = 21.93$, $p = 0.00174$).

Evenness

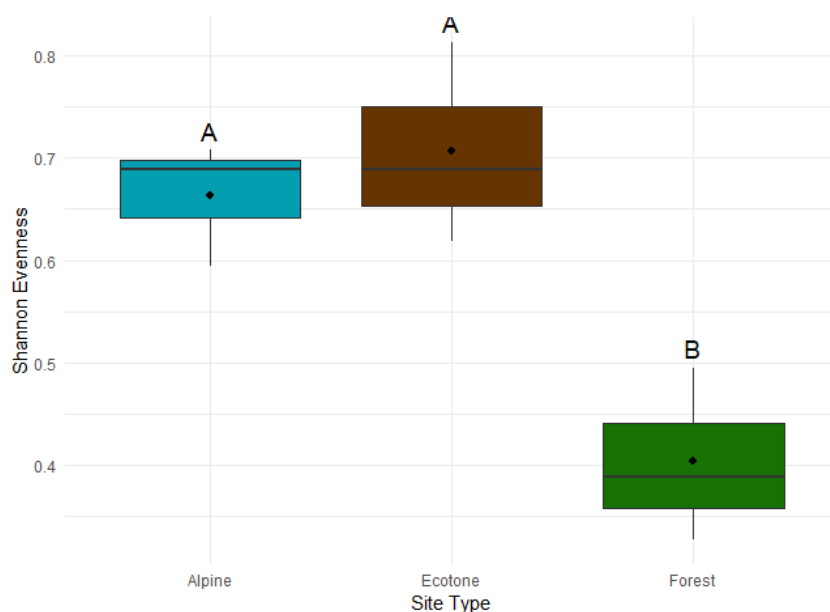
Evenness is a measure of how evenly individuals are distributed among the species present in a community (Figure 2.6). The results of the ANOVA for species evenness across site types indicated significant differences ($F(2, 6) = 10.64$, $p = 0.0106$), suggesting that site type does influence the evenness of species distribution. Alpine and ecotone sites exhibited similar

levels of species distribution evenness, indicating a similar competitive environment. In contrast, forest sites showed a large decrease in evenness, suggesting a few species – potentially including clonal plants – may dominate these ecosystems.

Further analysis of these differences through Tukey's HSD revealed that the difference in evenness between alpine and ecotone sites was not statistically significant (mean difference = 0.0499, $p = 0.7713$), indicating that the evenness of species distribution in these two site types is similar. However, significant differences were found when comparing forest sites to both alpine (mean difference = -0.2559, $p = 0.0265$) and ecotone sites (mean difference = -0.3058, $p = 0.0121$). Thus, the forest sites had a significantly lower evenness of species distribution compared to the other two site types.

Figure 2.6

Evenness by Site Type



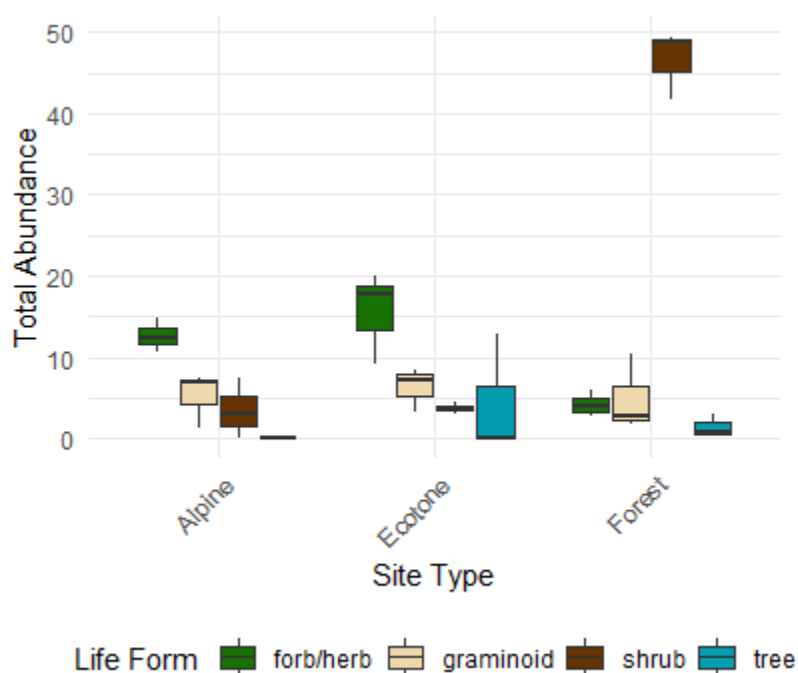
Notes. Boxplot showing the Evenness across alpine, ecotone, and forest site types. Means are plotted as points, and medians as bold lines. The overall ANOVA indicated significant differences in species evenness among site types ($F(2, 6) = 10.64$, $p = 0.0106$). Alpine and ecotone sites show no significant differences in species evenness ($p = 0.7713$), though forest sites are significantly different from both alpine ($p = 0.0265$) and ecotone sites ($p = 0.0121$).

Abundance of Life Forms

When considering the interaction between site types and life forms, the Kruskal-Wallis test revealed a significant effect (chi-square = 25.204, df = 11, p-value = 0.008509). This result confirms that the proportion of life forms varies significantly when both site type and life form are considered together (Figure 2.7). This finding illustrates the variation in ecological niches and competitive environments across the alpine, ecotone, and forest ecosystems. Specifically, the significant variation in life form abundance suggests that different environments favor certain growth strategies over others.

Figure 2.7

Abundance of Plant Life Form by Site



Clonal Dominance Analysis

PerMANOVA was conducted to relate various environmental factors to the dominance of clonality within a community (Table 2.4). This analysis investigates how much of the variation in clonal dominance is explained by each environmental variable.

The Ecosystem accounted for a substantial 77.73% of the variation in clonal dominance ($R^2 = 0.77773$) and was significant ($F = 18.3882$, $p = 0.017^*$), therefore, ecosystem has a significant influence on the clonal dominance in the community. The mountain, slope, and aspect were not significant, indicating that spatial location and physical characteristics of the terrain were not major factors influencing clonality in these communities, allowing us to attribute these differences to ecosystem.

Table 2.4

Permutational Multivariate Analysis of Variance (PerMANOVA) Results for Environmental Variables – Clonal Dominance

	Df	SumOfSqs	R2	F	Pr(>F)
Overall Model					
ES	2	0.63530	0.77773	18.3882	0.017*
Asp	1	0.13372	0.16370	7.7406	0.066
Slp	1	0.01313	0.01607	0.7600	0.541
Mt	2	0.00017	0.00021	0.0049	0.998
Residual	2	0.03455	0.04230		
Total	8	0.81686	1.00000		

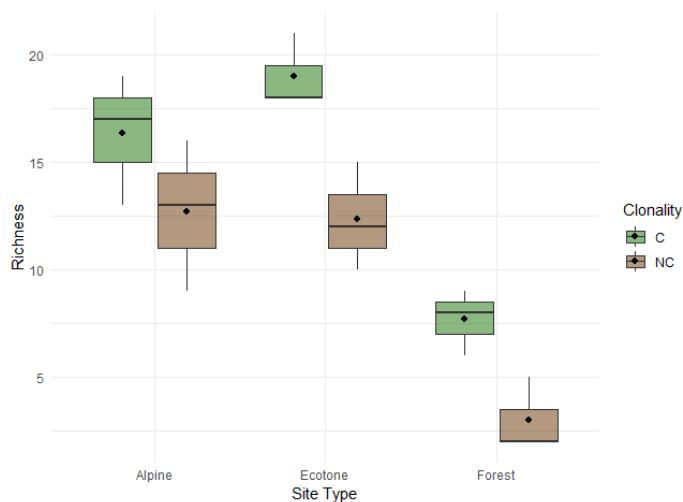
Notes. Environmental variables tested included ecosystem (ES), slope-aspect (Asp), slope (Slp), and mountain (Mt). This analyzed differences in clonal dominance by cover in relation to environmental variables. Asterisk identifies significant result at $\alpha < 0.5$.

Richness and Abundance – Clonality

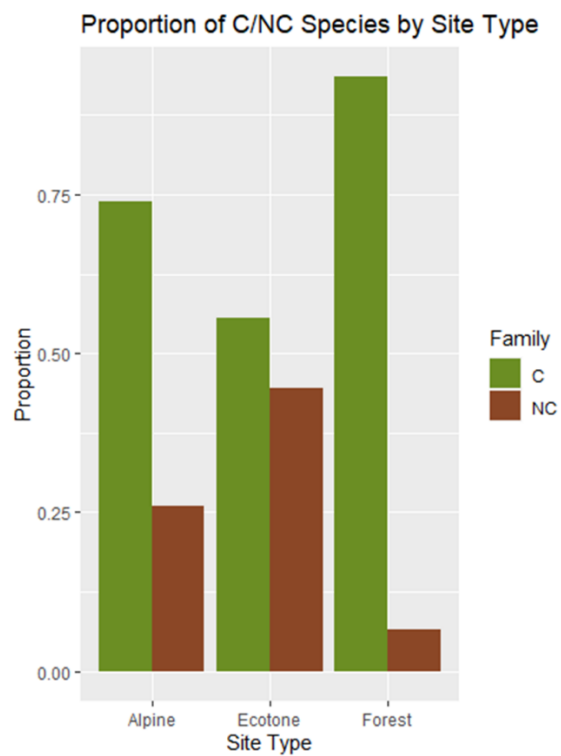
After assignment to clonal and nonclonal groups, richness was calculated again (Figure 2.8). Alpine sites exhibited richness between 13 to 19 for clonal plants and 9 to 16 for nonclonal plants, respectively. Ecotone sites also demonstrated substantial richness in clonal plants (18 to

21), compared to 10 to 15 for nonclonal plants. Forest sites showed a significant disparity between clonal and nonclonal plant richness, with clonal richness between 6 to 9 and nonclonal from 2 to 5. An ANOVA revealed significant differences in clonal richness across site types ($F(2, 6) = 21.55$, $p\text{-value} = 0.00183$). Tukey's HSD post-hoc test found significant differences between forest and alpine (difference = -8.6667 , $p\text{-adjusted} = 0.00716$) and forest and ecotone (difference = -11.3333 , $p\text{-adjusted} = 0.00185$), but not between alpine and ecotone sites (difference = 2.6667 , $p\text{-adjusted} = 0.3650$).

Next, we assessed abundances of plants assigned to clonal or nonclonal growth (Figure 2.9). The ANOVA revealed significant variations in clonal dominance among the site types ($F(2,6) = 6.116$, $p = 0.0356$). Tukey's HSD post-hoc test was performed to further investigate the differences between pairs of sites but showed no significant difference in the proportion of clonality between ecotone and alpine sites (difference = -0.1544 , $p\text{-adjusted} = 0.6029$), suggesting that these two site types do not significantly differ in the clonal versus nonclonal species composition. A notable difference was observed between forest and alpine sites (difference = 0.3706 , $p\text{-adjusted} = 0.1157$), although this difference was not statistically significant. A significant difference was found between forest and ecotone sites (difference = 0.5250 , $p\text{-adjusted} = 0.0333$).

Figure 2.8*Richness of Clonal and Nonclonal Plants by Site Type*

Notes. Means are plotted as points, and medians as bold lines.

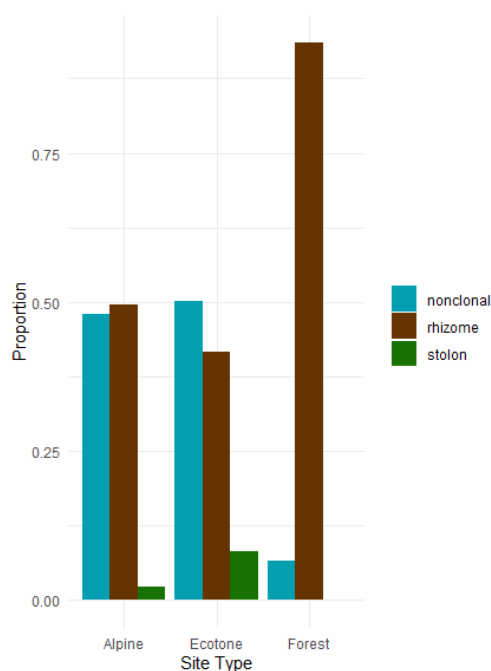
Figure 2.9*Proportion of Clonal and Nonclonal Species by Site Type*

Dominant Clonal Growth Organ

The Kruskal-Wallis rank sum test was used to assess whether the median arcsine-transformed proportions of clonality differ across the three site types (alpine, ecotone, and forest). This was chosen based on the Shapiro-Wilk test results, which indicated that the arcsine-transformed proportions did not follow a normal distribution for any of the site types. The analysis yielded a Kruskal-Wallis chi-squared value of 3.223 with 2 degrees of freedom, resulting in a p-value of 0.1996. This suggests that there is no statistically significant difference in the median arcsine-transformed proportions of clonal growth organs among the alpine, ecotone, and forest site types. Despite the lack of significant differences in the proportions of clonal growth organs among the site types, we still found that clonal plants were dominant within these ecosystems, particularly in alpine and forest sites where clonal strategies might be more advantageous (Figure 2.10).

Figure 2.10

Proportion of Dominant CGO by Site Type



Clonal Trait Analysis

Polygonum viviparum

Subsequent analysis of the number of buds across alpine and ecotone habitats utilizing a Two-Sample t-test revealed no significant difference in means ($t = 1.6587$, $df = 38$, $p\text{-value} = 0.1054$), with mean bud counts per individual of 1.1818 (alpine) and 0.7222 (ecotone) (Figure 2.11). However, ecotone sites showed a higher coefficient of variation (104.110%), while alpine sites showed a lower coefficient of variation (81.061%). This result suggests that, while there is a trend towards higher bud production in alpine habitats, this difference does not reach statistical significance, challenging Hypothesis 3 that clonal plants exhibit significant intraspecific trait variation across environmental gradients (Table 2.5).

Carex nardina

The analysis conducted on the *Carex nardina* trait data aimed to compare the mean number of buds per rooting unit and mean lateral spread between two habitat types, alpine and ecotone.

The Two Sample t-test comparing the mean number of buds between alpine and ecotone sites yielded a t-value of -0.03115 with 32 degrees of freedom, resulting in a p-value of 0.9753. This suggests that there is no statistically significant difference in the mean number of buds per rooting unit between alpine (mean = 0.6093985) and ecotone (mean = 0.6155556) site types, indicating minimal intraspecific variation in bud density across these gradients (Figure 2.12A). Alpine sites showed greater variability, with a higher coefficient of variation of 109.892%, compared to 67.360% in ecotone sites.

Similarly, the Two Sample t-test for mean lateral spread showed a t-value of 0.58951 with 32 degrees of freedom and a p-value of 0.5597. This result indicates that the difference in mean

lateral spread between alpine (mean = 11.615000) and ecotone (mean = 9.713333) site types is not statistically significant (Figure 2.12B), but we do see a trend of higher lateral spread in alpine ecosystems (Table 2.5). When assessing variance of lateral spread, ecotone sites had a higher coefficient of variation (95.664%) compared to alpine sites (80.725%).

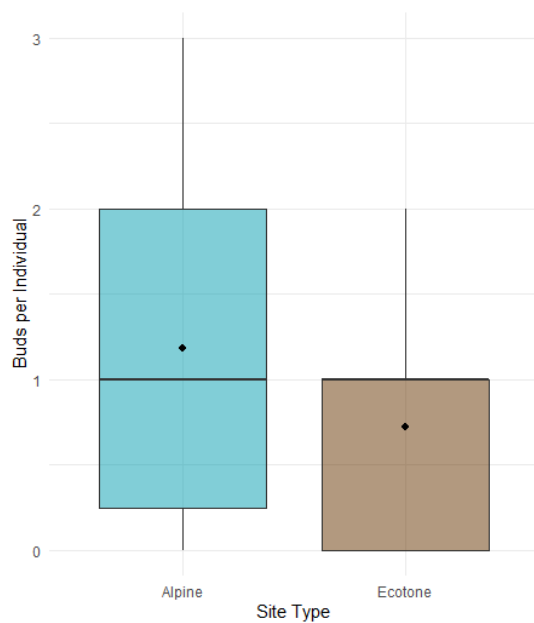
Table 2.5

Trait Analysis of Selected Species

	t-value	p-value
<i>Carex nardina</i> – Mean Lateral Spread	0.58951	0.5605597
<i>Carex nardina</i> – # Buds per Rooting Unit	-0.03115	0.9753
<i>Polygonum viviparum</i> - # Buds per Individual	1.6587	0.1054

Figure 2.11

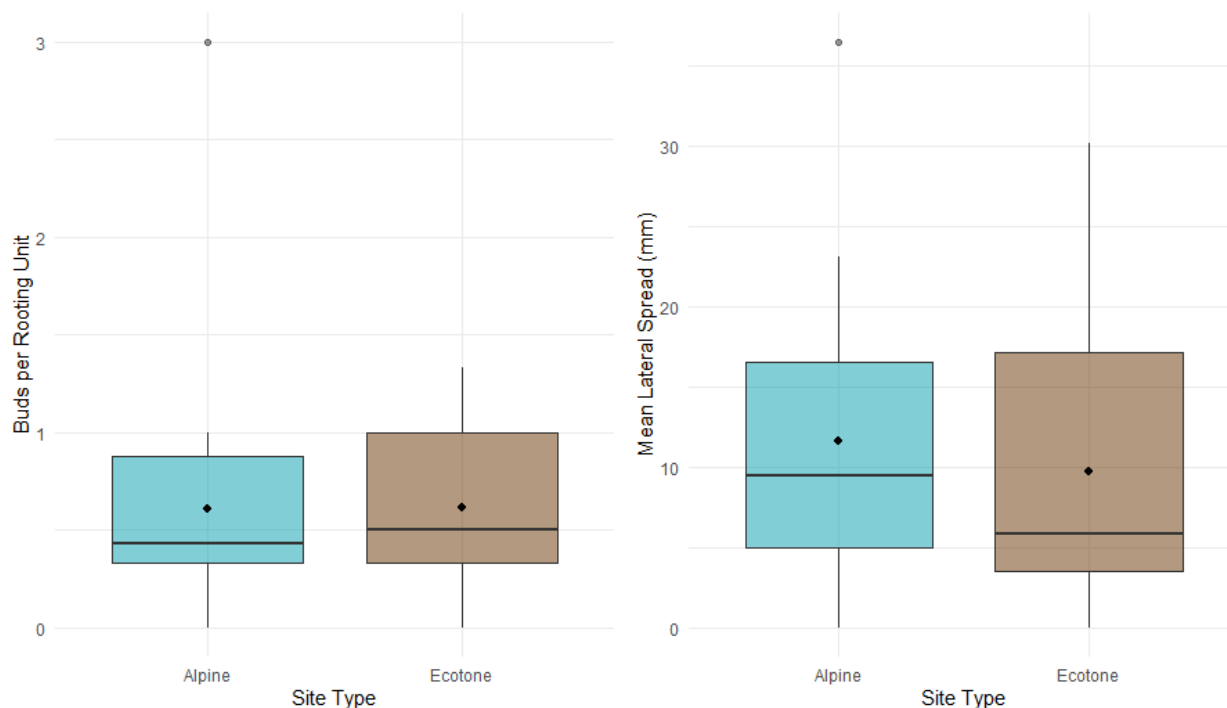
Box plot for Buds per Individual by Site Type in Polygonum viviparum



Notes. Means are plotted as points, and medians as bold lines.

Figure 2.12

Box plots for Buds per Rooting Unit (A) and Mean Lateral Spread (B) by Site Type in Carex nardina



Notes. Means are plotted as points, and medians as bold lines.

Discussion

Our findings offer significant insights into the impact of environmental gradients on plant dominance and clonality, confirming Hypothesis 1, that community composition changes significantly across the elevational gradient, with ecosystem type exerting substantial influence. This variation illustrates the importance of abiotic factors in shaping community structures and supports the idea that distinct ecosystems possess unique compositions of species adapted to specific environmental conditions. The finding is corroborated by Litaor et al. (2008), who demonstrated that snow distribution and subsequent soil moisture levels influenced herbaceous alpine vegetation diversity on Niwot Ridge. Furthermore, Winkler et al. (2016) highlighted the

role of soil moisture in mediating alpine life form and community productivity responses to warming on Niwot Ridge, further illustrating the interaction between abiotic factors and ecosystem adaptation to changing climates.

The clear distinction in species composition across different ecosystems, particularly between alpine and forest sites, supports the use of mountain ecotones as focal areas for studying ecological transitions (Niu et al., 2019) and clonal dominance. We found partial support for Hypothesis 2, in which clonal plants will be more dominant in alpine and forest ecosystems, a trait that may improve resilience and adaptability of these species in harsh environments. Rosbakh and Poschod (2021) demonstrated that persistence strategies like soil seed banks, adult longevity, and clonality vary along an elevational gradient, with adult longevity being particularly prominent in alpine communities. This is further supported by Silvertown (2008), where evidence of increased clonality in older populations and at the edges of geographical ranges was found.

Our study found that the ecotone has the highest richness of clonal plants, though they also had the lowest proportion of cover. We found that clonal plants were dominant in alpine and forest ecosystems, with our analysis showing a significant proportion of clonal species in the communities, as anticipated. This finding aligns with our second hypothesis and highlights the role of clonality as a strategy for survival and reproduction in environments where climatic conditions or competition may limit sexual reproductive success. The prevalence of clonal growth in these ecosystems might reflect an adaptation to environmental stressors and interspecific competition, offering a competitive advantage in resource acquisition and survival.

Trait Variation

We found a lack of significant differences in the proportions of dominant clonal growth organs among the site types of our study. Herben and Klimešová's (2020) research suggests that the evolutionary flexibility of clonal growth organs allows plants to adapt to diverse ecological niches, overcoming constraints by adjusting their morphologies. However, the lack of significant differences in the proportions of dominant clonal growth organs among the site types in our study further suggests that clonality might be influenced by factors beyond just the environmental gradient.

The study also investigated the intraspecific variation in clonal traits across the environmental gradient, addressing the hypothesis that clonal plants exhibit significant trait variation. We expected responses to differing environmental pressures encountered across the gradient to result in clonal trait variation. While our results did not align with our initial expectations, they contribute valuable information to the field, specifically by serving as a foundation for future research to build upon.

We saw a trend towards higher bud production of alpine *Polygonum viviparum*, but this was not significant. Evette et al. (2009) and Qian et al. (2017) observed an increase of bud bank size with increasing elevation. Additionally, Dalgleish and Hartnett (2006) suggest that bud banks increase along a precipitation gradient. These findings support the trend that we observed in *Polygonum viviparum* despite the lack of significance.

However, the findings of *Carex nardina* traits deviate from the literature. We observed a nonsignificant trend indicating more lateral spread in alpine individuals, though the literature suggested a decrease. Rosbakh and Poschlod (2021) documented a decrease in lateral spread with increasing elevation while Evette et al. (2009) reported that species with a high rate of lateral spread were less dominant in alpine environments.

We also observed increased variability in *Polygonum viviparum* buds and *Carex nardina* lateral spread in the ecotone sites, though *Carex nardina* buds had increased variability in alpine sites. These findings could reflect the broader range of ecological conditions and adaptive strategies necessitated by the fluctuating and extreme high-altitude environments. This variability in plant trait may be due to diverse microclimates. However, this rationale goes against our initial hypotheses that ecotones will have less clonal growth because they are more disturbed than alpine sites.

It is possible that our study did not include enough plots investigated or a large enough number of individuals to adequately represent the variability within species. Larger sample sizes could increase the likelihood of detecting significant trait variations, though our findings lay the groundwork for future research. This contribution is especially valuable in light of the difficulties in accessing detailed trait data for clonal plants. By sharing our observations and data, we aim to support and encourage further studies to gain a more comprehensive understanding of clonal trait variations.

Implications and Future Directions

The observed patterns of plant dominance, clonality, and intraspecific trait variation across the environmental gradient offer valuable insight into the adaptive strategies of plant communities in response to climate change. The finding that a warming climate could lead to shifts in community compositions reinforces the need to consider clonal growth as a potentially advantageous trait in predictive models of vegetation dynamics.

However, a notable challenge in our study was the lack of comprehensive trait information for clonal species, which limited our ability to classify clonal species and the records of dominant CGO across different habitats. This gap underscores the need for more extensive

databases and detailed trait measurements to better understand the ecological strategies of clonal plants.

Moving forward, it will be crucial for future research to focus on filling the gaps in trait data, particularly for clonal species in diverse habitats. Integrating comprehensive trait databases with detailed field measurements can significantly enhance our understanding of clonal strategies and their contributions to ecosystem resilience. Moreover, such data are vital for predicting community responses to ongoing environmental changes.

CHAPTER III

SYNTHESIS, FUTURE DIRECTIONS, AND CONCLUSIONS

Summary of Conclusions

This thesis aimed to explore the patterns of dominance and distribution among clonal species across environmental gradients in the Colorado Front Range, employing a trait-based comparative analysis to understand the adaptive strategies of alpine flora and their implications for conservation amid rapid climate change. As a dominant strategy in Colorado's alpine flora, clonal growth offers insights into plant adaptation, survival, and community dynamics under changing climatic conditions. We structured our investigation around three core research questions and corresponding hypotheses to achieve a comprehensive understanding.

We aimed to address the following research questions and hypotheses:

Research Questions

- Q1 How does plant dominance change across the environmental gradient?
- Q2 How does clonal dominance change across the environmental gradient?
- Q3 How does intraspecific clonal trait variation change across the environmental gradient?

Hypotheses

- H1 There will be a change in community composition across the gradient.
- H2 In alpine and forest ecosystems, clonal plants will be dominant in cover.
- H3 Clonal plants exhibit significant intraspecific trait variation across environmental gradients.

Through the collection of vegetation cover data from nine sites and subsequent analysis, our goal was to delve deep into the adaptive strategies of clonal plants. Our analysis utilized PerMANOVA and MRPP for community composition assessment, complemented by species richness and diversity indices to gauge biodiversity across gradients. We then performed trait analysis for two measured traits of each species.

Our results, derived from PerMANOVA and MRPP analyses, demonstrate significant variations in community composition influenced by ecosystem types and elevation. These findings substantiate our first hypothesis (H1), highlighting the pivotal role of elevation and ecosystem delineations in structuring plant communities across the Front Range. Our findings are supported by Litaor et al. (2008) and Winkler et al. (2016) who demonstrated the importance of soil moisture levels in alpine community diversity and productivity at Niwot Ridge. The work of Sundqvist et al. (2013) provides a complementary and supporting perspective by investigating the role of elevational gradients on community structure and ecosystem processes. Niu et al. (2019) also support the use of mountain ecotones as areas to study ecological transitions as a space-for-time substitution. Their research accentuates the role of temperature as a major factor driving the diverse responses observed across various gradients, while also underscoring the utility of elevational gradients in predicting climate change responses of plant communities. Together, these studies enrich our understanding of elevation and ecosystem types as key drivers of plant community dynamics, offering valuable context for our observations within the Front Range's unique environmental gradients.

Hypothesis 2 suggested that clonal plants would be more dominant in alpine and forest ecosystems. Our findings partially support this hypothesis, demonstrating the highest richness, but lowest proportion of clonal species in ecotones.

Silvertown (2008) explained that clonal reproduction frequency increases with population age, suggesting that disturbance limits clonal growth. Given that ecotones are characterized by more frequent disturbances, this supports our finding that ecotones have less clonal dominance. However, Silvertown (2008) also found increased clonality at the edge of geographical ranges, such as those found in the ecotone. This complicates the results further and brings into question whether disturbance or climate influences clonal dominance more.

Further, the preference for clonal over nonclonal plants species in colder temperatures, as observed by Klimeš et al. (1997), highlights the adaptability of clonal species to alpine regions. This is attributed to dominance or abundance of clonal species and not necessarily the number of clonal species, though our findings show higher values of clonal species for both richness and abundance. However, Klimeš (2003) noted a decline in clonal plant species with increasing elevation in the Trans-Himalaya, suggesting that the relationship between clonality and elevation is complex and potentially limited by species' abilities for clonal growth.

The heterogeneity and resource-rich nature of forest ecosystems further compound the advantages of clonal growth. Studies like Herben (2004) highlight how clonal plants, through physiological integration and resource translocation, can significantly alter their growth form and exhibit superior competitive abilities in heterogeneous environments. This is echoed by Wang et al. (2021), who found that physiological integration enhances the biomass of both donor and recipient ramets in heterogenous environments. Cao et al. (2022) also indicate that clonal integration influences clonal plants' foraging behavior, although the effectiveness of this strategy varies significantly among species.

The forest-alpine ecotone of Colorado serves as a prime example of the dynamic nature of ecotones. Humphries et al. (2007) describe the ecotone of Niwot Ridge as exhibiting varied

spatial patterns of tree species influenced by environmental factors, with distinct vegetation patterns emerging based on the degree of topographic heterogeneity and disturbance. This variability suggests that ecotones may not uniformly support clonal growth due to their environmental variability and disturbance regimes, contrasting with more stable and resource-rich forest ecosystems.

The interaction between disturbance frequency, site productivity, and plant reproductive strategies further clarifies this dynamic. In environments where disturbances are frequent and productivity is low, clonal plants can be outcompeted by short-lived seeding plants, as noted by Bellingham and Sparrow (2003). Simpson et al. (2021) provide additional support, associating resprouters with less frequent disturbances than seeding plants, reinforcing the notion that disturbance regimes play a critical role in determining the success of clonal growth strategies. Overall, these studies support our hypothesis that clonal plants are more dominant in alpine and forest ecosystems than in ecotones (H2) and also provide support for our findings.

Our study aimed to understand how intraspecific clonal traits change across environmental gradients. However, the patterns observed in our analysis were not straightforward, revealing complexity that challenges our initial hypothesis (H3) that clonal traits will change along the elevation gradient. In the case of *Polygonum viviparum*, a trend was observed towards an increased bud bank size within alpine habitats, albeit lacking statistical significance. This trend corroborates with studies such as those by Evette et al. (2009) and Qian et al. (2017), which documented an increase in bud bank size with elevation and the associated harsher conditions. This species also had one individual possessing bulbils, suggesting that there are diverse strategies of clonal reproduction present.

Conversely, *Carex nardina* presented findings that deviate from patterns in the literature. While we observed a trend indicating greater lateral spread among alpine individuals of *Carex nardina*, this finding contradicts expectations based on the literature and was not statistically significant in our study. Evette et al. (2009) and Pokarzhevskaya (1995) revealed that species exhibiting a high rate of lateral spread contribute less to overall cover in alpine environments. Rosbakh and Poschlod (2021) add to this by documenting a decrease in lateral spread with increasing elevation.

However, this may be explained by the impact of disturbances on clonal growth. Bellingham and Sparrow (2003) observed that in areas with frequent disturbances and low productivity, resprouters are outcompeted by short-lived seeding plants. Additionally, the adaptive mechanisms for lateral spread in *Carex nardina* might operate differently from those documented in existing research, or that other ecological factors not captured in our study may influence these patterns. Additionally, our investigation into the species' bud density revealed no difference across gradients, further complicating the understanding of clonal adaptation in varying environmental conditions.

These observations, particularly the consistent trend in bud bank size for *Polygonum viviparum* aligning with literature, contrasted with the unexpected and non-significant trend in lateral spread for *Carex nardina*, highlight the complexity and variability of clonal plant strategies in response to elevation and other environmental factors.

Limitations and Future Research Directions

Our study encountered several limitations that highlight areas for future research. First, our study focused on evaluating the impact of broad-scale environmental gradients on clonal growth strategies. While this approach helps identify general trends, it may not consider the

nuanced effects of microclimate conditions on individual plant responses. These microhabitats can have unique soil moisture, light availability, and temperature variations, significantly influencing clonal trait expression and success. Our data collection was constrained to a single field season, further limited by the necessity to wait for snowmelt and the commencement of spring plant growth. Future research should prioritize collecting and analyzing fine-scale environmental data to overcome this limitation. Ecotonal areas are of particular interest due to the overlapping of communities and the extent of survival. This stress may induce trait variation within a species.

The idea of clonality as an adaptive mechanism is complex and requires further exploration. However, it is unknown how likely different species are to use clonality in various habitats or which specific clonal growth organs (CGOs) dominate in certain environments. To investigate this further, future studies should aim to quantify the probability of clonal reproduction across different environmental conditions. Since species can possess multiple CGOs, these should be identified and quantified to assess which are dominant in a given ecosystem. These studies could involve field observations, controlled greenhouse or growth chamber experiments, or modeling approaches to understand the ecological factors at play better.

One of the significant challenges faced while conducting trait-based analyses and ecological modeling efforts is the limited availability of detailed clonal trait data, especially for species in the United States and alpine ecosystems. This scarcity of data results in an incomplete understanding of clonal plant biology. To address this issue, an effort must be made to compile and share clonal trait data.

Although our study highlighted the significance of clonality in plant adaptation, it did not explore the genetic variation within clonal populations. Genetic diversity plays a crucial role in

the resilience and adaptability of populations, determining their ability to respond to environmental changes. By incorporating genetic analyses such as genotyping by sequencing or whole-genome sequencing, we can acquire valuable insights into the genetic structure of clonal populations. Such analyses will provide a better understanding of the role of genetic diversity in clonal adaptation and resilience, leading to a fresh perspective on conservation strategies for clonal plant species in evolving environments.

Addressing the limitations and pursuing the suggested future research directions can significantly enhance our knowledge of clonal growth strategies and their ecological implications. This will help us develop more precise and effective conservation efforts in the face of global environmental change.

The Role of Clonal Growth in Alpine Community Resilience

As we move forward, it becomes increasingly important to advance trait-based ecology. Our research helps this endeavor by shedding light on how clonal growth strategies adapt to environmental changes. The significant variability in community composition that we observed suggests we must reassess how trait-based models predict species responses to climate change. Future studies should aim to explore the complex and intricate relationships between clonal growth mechanisms and the specific environmental conditions of their habitats. Future research must investigate factors such as elevation, temperature, moisture availability, and disturbance regimes to improve our ability to model and predict ecological responses accurately.

Our findings also highlight the role of clonal growth in ecosystem dynamics and plant community structure. Clonal strategies, such as physiological integration and varied reproductive tactics, offer plants a competitive edge in both homogenous and heterogenous environments. Incorporating these clonal traits into ecological models will enhance our ability to forecast

changes in vegetation patterns and ecosystem services under future climate scenarios.

Additionally, the observation that clonal growth strategies differ not just between but also within species across environments calls for an in-depth approach to trait analysis.

Applying our research findings to broader ecological contexts extends the potential impact of our work beyond alpine flora. The adaptability of clonal plants in diverse ecosystems suggests that studying clonal growth strategies can provide valuable insights into ecological resilience, competition, and succession in various environments. Therefore, integrating detailed trait data, genetic diversity, and the effects of clonal integration on plant competition and resource utilization into ecological studies is essential.

The Use of a Mountain Elevation Gradient as a Model System

Using a mountain elevation gradient as a model system in ecological research offers a compelling method to explore the effects of elevation on biodiversity and ecosystem processes. This approach provides a natural laboratory where researchers can examine the impacts of elevation on biotic responses and evolutionary adaptation over relatively short spatial distances. These gradients are characterized by distinct changes in environmental conditions, such as temperature, moisture, and light availability, which affect the distribution and adaptation of organisms.

However, interpreting results from studies using elevation gradients can be challenging because the gradients often include environmental changes that reflect local variations and not attributable to elevation. It is crucial that we distinguish between environmental drivers associated with elevation, like atmospheric pressure and temperature, and those not elevation-specific, such as moisture and human land use. We attempted to reduce these by critically choosing the sites and plot locations. Additionally, incorporating detailed environmental data,

including fine-scale climate and soil moisture measurements can enhance the understanding of how elevation influences ecological and evolutionary processes.

While mountain elevation gradients offer valuable insights into ecological and evolutionary dynamics, their effectiveness depends on a holistic understanding of the interplay between elevation-specific and non-specific environmental factors. By addressing these challenges, elevation gradients can continue to serve as a powerful tool for advancing ecological research and contributing to our understanding of biodiversity patterns and ecosystem functions across the world's mountainous regions.

Concluding Remarks

This thesis not only emphasizes the intricacy of clonal growth strategies and their interplay with environmental gradients but also illustrates the adaptability of clonal plants to diverse ecosystems. It advocates for a trait-based approach and pushes the limits of current ecological models. By doing this, we unlock new possibilities for comprehending and preserving biodiversity in the face of global change. The integration of comprehensive trait data and genetic analyses stands as a testament to the evolving nature of ecological research, advocating for an in-depth examination of plant strategies across various ecosystems. This methodology enhances precision in our predictions and interventions in the face of climate change and habitat degradation. As we move forward, it becomes imperative that we adopt and refine these approaches to better understand the ecological dynamics of our native ecosystems, ensuring a resilient and diverse world for future generations.

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